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Genetic analysis of ear length and correlated traits in maize

by

Andrew Jon Ross

A dissertation submitted to the graduate faculty

in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Major: Plant Breeding

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For the Major Program

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ABSTRACT

Maize (*Zea mays* L.) ear length is positively correlated with grain yield. Thirty generations of selection for increased ear length, however, failed to increase grain yield in Iowa Long-Ear Synthetic (BSLE). Negative correlations between ear length and other yield-related traits complicated indirect selection for grain yield. The main objective of this investigation was to identify quantitative trait loci (QTL) that affect the variation of ear length, grain yield, and other ear traits, and the correlations among traits. Secondary objectives were to validate QTL by comparing their genetic positions across generations, environments, and other populations. QTL were mapped in the F_2 and $F_{2:3}$ generations of a bi-parental population. The inbred parents differed in ear length by 14 cm, and were derived from the divergent sub-populations of BSLE.

More QTL were detected for ear length (16), kernel-row number (12), and kernel depth (6) than detected in prior QTL studies. Eighty percent of the alleles for increased trait values originated from the parent with the higher trait value. Most QTL were validated by one of three methods. More than 67% of the QTL were identified in at least two $F_{2:3}$ environments. Forty-three percent of the QTL from the $F_{2:3}$ mean environment were previously identified in the F_2. Seven QTL for ear length, one for kernel-row number, and two for grain yield seemed to coincide with QTL in other populations. Traits with higher heritabilities generally had more coincidental QTL, and traits with lower heritabilities generally had fewer coincidental QTL.

QTL positions and the parental origin of alleles agreed with the direction of the genetic correlation coefficients. The magnitude of the correlations was generally explained by the frequency of QTL that coincided or were genetically linked. Repulsion-phase linkage between ear length and grain yield QTL near the centromere of chromosome 5 may have caused the failure of ear length selection in BSLE to increase grain yield. QTL on chromosome 6 exemplified the genetic basis for the positive correlation between ear length and grain yield.

CHAPTER 1.
GENERAL INTRODUCTION

Introduction

Increasing the grain production of crop species is the primary objective of many plant breeding programs. Grain yield is a culmination of the development of many plant structures and their interaction with environmental signals. The complexity of the grain yield phenotype makes it less predictable than other traits. Thus, grain yield is often partitioned into components or traits that have explanatory value for predicting grain yield. The genetic correlations of grain yield with yield components suggest that selection on individual components may be used to indirectly increase grain yield. The mix of positive and negative genetic correlations between yield components often decreases the success of increasing grain yield by selecting on a single component.

In maize (*Zea mays* L.), a notable yield component is the length of the female inflorescence or ear shoot. A long-term divergent selection experiment conducted in the Iowa Long Ear Synthetic (BSLE), however, displayed the inability of selection solely on ear length to increase grain yield (Hallauer et al. 2003). The correlated response of other yield components, such as kernel-row number and kernel depth, with selection for shorter and longer ears indicated that the advantage of longer ears was countered by a decrease in these traits.

The number and effect of genes controlling ear length and other yield components and the interaction of these genes to produce trait correlations has mainly been estimated from studies focusing only on trait phenotypes. Information and conclusions obtained from these studies are limited when the genetic cause of trait variation is unknown. The location and effect of genetic regions or quantitative trait loci (QTL) affecting trait variation should provide a more comprehensive understanding of the inheritance and correlations among traits.

The research in this dissertation was completed to gain information on the genetic cause of trait inheritance and correlations. The primary trait of interest was ear length, but traits correlated with ear length also were studied. This research utilized germplasm from the BSLE divergent selection experiment. The long- and short-ear generation 24 sub-populations of BSLE differ in mean ear length by ≈ 14 cm, and are divergent for other grain yield components with respect to their correlation with ear length. An F_2 population was developed from inbred parents derived from the BSLE generation 24 sub-populations to map QTL for ear length, grain yield, and other yield components. Previous studies have used bi-parental populations derived from elite inbred lines to

map QTL for these traits. The divergence of ear length and other yield related traits in BSLE should increase the chances of identifying QTL (Lander and Botstein, 1989; Falconer and Mackay, 1996).

The primary objectives of this dissertation were to determine the genetic positions and effects of QTL affecting ear length and traits correlated with ear length, and identify QTL with stable effects on trait variation across generations and environments. Secondary objectives were to validate QTL by comparing across populations previously used to study grain-yield components, and to determine the positions of QTL that may cause trait correlations.

Dissertation Organization

This dissertation consists of four chapters and accompanying appendices. The remainder of the first chapter provides a review of literature relevant to the research presented in this dissertation. The second and third chapters were prepared as manuscripts to be submitted to *Crop Science*. The second chapter describes the genetic mapping of QTL for ear length and a component of ear length that may partially explain variation for EL in the F_2 and $F_{2:3}$ generations of a bi-parental maize population. The third chapter describes the detection of QTL for grain yield and ear traits correlated with ear length in the same population and generations used in chapter two. The fourth chapter includes the general conclusions relevant to the results of chapters two and three. A complete list of literature referenced throughout the dissertation is included at the end of chapter four.

Literature Review

Maize Inflorescences and Botanical Terms

Zea mays is a member of the grass family, *Gramineae*, and partitioned into the tribe *Maydeae*. Maize is monoecious and has imperfect flowers separated in to male and female floral structures. The male inflorescence, or tassel, of maize terminates the primary shoot (main stem). The female inflorescences, or ears, terminate the secondary shoots (ear shoots) (Kiesselbach, 1999) present at each aboveground node of the primary shoot, except for the six to eight nodes prior to the tassel (Ritchie et al., 1996). The tassel and ear structures, despite their perceived diversity, are rather homologous. Several homologies were reported by Anderson (1944) and included 1) the correlation of spikelet density of the tassel to the number of rows of kernels on the ear, 2) the correspondence between tassel branch length and ear length, and 3) the relative lengths of successive tassel branches to the shape of the ear (e.g., cylindrical, conical, and pear-shaped). Detailed descriptions of the development and structure of maize inflorescences were provided by Kiesselbach (1999), Bonnett (1948), and Lenz (1948).

The structure of maize inflorescences is often described using terms specific for the crop, but botanical terms are universal. The correspondence between the two terminologies is briefly addressed, with focus on the ear shoot, for knowledge and comprehension of traits mentioned in further portions of this dissertation. The mature ear generally is characterized by its length and the number of vertical kernel rows. The length of the ear is a product of the number of cupules per rank and the distance between cupules. Cupules are cup-like depressions or alveolus (Lenz, 1948) along the ear's rachis (cob), in which pairs of spikelets (kernels after pollination and maturation) are attached. The pairing of spikelets within cupules provides the ear with an even number of kernel rows. Half the number of kernel rows or the number of vertical rows of cupules is considered the rank of an ear.

BSLE Long-Term Selection Experiments

BSLE was developed by crossing the double-double crosses of 12 inbreds in all possible combinations followed by three generations of random mating. The 12 inbreds with above-average ear length were B50, B55, B56, B217*wx*, C103, N22A, N25, Oh29, W-17R-B, (B15/B18)-16, (Lancaster Comp.)-34, and (L317/187-2)-1-1-9 (Russell et al., 1971). Based on pedigree information, BSLE is approximately 34% Reid Yellow Dent (Reid, Funks, Osterland, and Iodent), 23% Lancaster Sure Crop, 13% Krug Yellow Dent, 4% Midland Yellow Dent, 4% Alph, 11% other open-pollinated varieties or breeding synthetics, and 11% undetermined germplasm.

Phenotypic plant selection (mass selection) for divergent ear length in BSLE was initiated in 1963 using a grid system (Gardner, 1961) to select shorter [BSLE(M-S) sub-population] and longer [BSLE(M-L) sub-population] maize ears. Hallauer et al. (2003) and Lopez-Reynoso and Hallauer (1998) provide details of the two sub-populations advancement through more than 27 cycles of mass selection.

To estimate the total genetic (σ^2_G), additive genetic (σ^2_A), and dominance (σ^2_D) variances for ear length (EL), ear diameter (ED), kernel-row number (KRN), kernel weight (KWT), grain yield (GY), and several other agronomic traits, a Design I mating scheme was employed using plant material from BSLE cycle (C) zero (Hallauer, 1968). In the combined analysis of variance, σ^2_A was large and significant, but the σ^2_D was negative (zero or small variance estimate) for EL, ED, KRN, KWT, and GY. The genetic correlation coefficient (r_g) and additive genetic correlation coefficient (r_a) for EL with ED and KRN were approximately –0.40. The r_g between EL and GY was 0.38, but the r_a was only 0.03. The coefficient of simple determination indicated that the phenotypic variation in GY attributable to EL was low (0.20).

Cortez-Mendoza and Hallauer (1979) reported the direct and correlated responses after 10 cycles of divergent mass selection in BSLE. The direct response of mass selection for divergent EL was asymmetrical, with an EL increase in BSLE(M-L) of 0.32 cm cycle^{-1} and a decrease of 0.64 cm cycle^{-1} in BSLE(M-S). The authors suggested the asymmetrical response was due to dominant gene action for alleles that increased EL, and the unequal allele frequencies in BSLE C0 that favored increased EL. The correlated responses with increased EL were a decrease in ED and kernel depth (KD). Selection for decreased EL was not accompanied by changes of other traits except for a decrease in GY.

After 15 cycles of divergent mass selection, Salazar and Hallauer (1986) estimated the σ^2_G present in BSLE C0, BSLE(M-L) C15, and BSLE(M-S) C15, and evaluated the C0, every third cycle of selection for each sub-population, and the crosses between the sub-populations at every third cycle. The authors found that the σ^2_G was maintained in each sub-population after the 15 cycles of selection. The linear regression coefficient (*b*) was computed for 10 agronomic traits across cycles of selection for the two sub-populations. Selection for increased EL was associated with a significant decrease in ED, KRN, KD, and GY, and the *b* value increased for plant height and female anthesis. Significant negative *b* values were obtained for GY, ear number per plant (ENP), plant height, and female anthesis, whereas ED, cob diameter, KRN, and KD had significant positive *b* values with selection for shorter ears. Significant heterosis for EL was observed in crosses between the sub-populations, suggesting that some level of dominance is present for expression of EL and that the sub-populations have different frequencies of alleles affecting EL.

Lopez-Reynoso and Hallauer (1998) conducted an experiment similar to that reported by Salazar and Hallauer (1986), but included 27 cycles of selection for divergent EL. Similar to Salazar and Hallauer (1986), the authors reported maintenance of adequate σ^2_G in both cycle 24 sub-populations and asymmetrical selection trends. Heterosis for EL was not observed by Lopez-Reynoso and Hallauer (1998). After 24 cycles of mass selection, EL increased by 5.4 cm in BSLE(M-L), and decreased by 8.7 cm in BSLE(M-S), providing a difference of 14.1 cm in EL between the two sub-populations of BSLE. Ear and kernel traits correlated with EL showed responses similar to the regression coefficients reported in previous investigations of the BSLE sub-populations.

Hallauer et al. (2003) summarized the preceding studies in BSLE and provided details on the advancement of the divergent sub-populations through 30 cycles of mass selection. The main results and conclusions from the BSLE long-term selection experiment were 1) EL was successfully modified by mass selection for longer and shorter ears, 2) GY was significantly reduced in BSLE(M-

S) but was not increased in BSLE(M-L), 3) the correlated responses of other ear traits, especially KD, likely explained the lack of a correlated response for GY due to selection for increased ear length, 4) the heritabilities of, and correlation between, EL and GY in BSLE indicated indirect selection for GY was inferior to selection on GY *per se*. Hallauer et al. (2003) addressed the explanations for the asymmetrical response to selection for EL. The effects of inbreeding and genetic drift were not likely explanations. The effective population size in each sub-population was at least 4,000 individuals, and parental control was minimized with selected plants being fertilized with pollen from selected and unselected plants. The most likely explanation for the asymmetrical response was that the frequencies of alleles for increased EL were presumably greater than 0.5 because BSLE was formed from long-eared inbreds. A secondary reason was that selection differentials may have differed because of pollen fertilization, scale effects, natural selection, and field techniques, (e.g., plant density, and nutrient management).

Correlation of Ear Traits

Hallauer and Miranda (1988) reported that EL is an important component of maize GY. The authors stated that several other ear and kernel traits could be considered maize yield components because of their positive genetic correlation with GY. The average r_gs from estimates in relevant literature were compiled by Hallauer and Miranda (1988; their Table 5.16). The average r_g with GY was 0.38 for EL, 0.41 for ED, 0.51 for KD, 0.24 for KRN, and 0.25 for KWT. Correlations between yield components does not allow for improvement of one without indirect affects on another. For example, the average r_g of KD and KRN with EL were ≈ -0.17.

Inheritance of Ear Length

A summary of 36 published estimates of genetic variances for EL was provided by Hallauer and Miranda (1988; their Table 5.1) and they concluded that additive variance was primarily responsible for EL variation and concurrently the average level of dominance was low indicating additive to partial-dominance types of gene action. Gardner et al. (1953), Williams et al. (1965), and Robinson et al. (1949) suggested the average level of dominance for EL was high and estimated gene action that ranged from partial- to over-dominance. Additional studies indicated epistasis affects the heredity of EL (Darrah and Hallauer, 1972; Wolf and Hallauer, 1997). The type of plant germplasm evaluated may influence the estimates of genetic variances and effects. Lamkey et al. (1993) noted that studies estimating genetic effects in synthetics and open-pollinated varieties of maize found additive effects to be more prevalent than dominance or epistatic effects. They indicated that studies involving crosses between elite inbred lines showed that epistasis and/or dominance were more important than additive effects.

Regardless of the type of plant material evaluated, evaluations of quantitative traits using biometric techniques provide only genome-wide averages of genetic effects. Biometry cannot identify the chromosomal locations of alleles that effect quantitative traits or estimate the effect of an allele (Lamkey and Lee, 1993). Molecular investigations have aided the comprehension of EL inheritance by attributing observed variation to partitioned regions of the maize genome and estimating the genetic effects that affect EL heredity. The evaluation of EL heredity in molecular investigations, however, has been a secondary objective to identifying genetic regions that contain genes directly affecting GY.

Genetic Analyses of Ear Length and Traits Correlated With Ear Length

Molecular investigations have been conducted using isozyme, restriction fragment length polymorphic (RFLP), and simple sequence repeat (SSR) marker loci to detect QTL that affect the variation of GY and yield components (EL, ED, KRN, KD, and ENP). Stuber et al. (1987) and Edwards et al. (1987) evaluated more than 1700 F_2 plants from each of two populations developed by crossing inbred lines from the southern United States to lines developed in Canada. The maps developed for these two populations had less than 20 isozyme markers and only 40% of the maize genome was within 20 centimorgans (cM) of marker loci. In these studies, most traits were associated with more 50% of the marker loci in each mapping population. Abler et al. (1991) used an average of 15 isozyme markers to map QTL in six populations having 504 F_2 plants each. On average, three chromosomes in each mapping population were without marker coverage. The authors identified several QTL affecting many yield components and determined the gene action present at those genomic regions. They reported that over-dominance was the most prevalent gene action for EL and GY, but attributed this result to repulsion phase linkage of two or more QTL to a marker locus.

Marker-trait associations were determined for EL and other morphological and agronomic traits, including GY, from the genotypes (98 RFLP and 14 isozyme loci) and the phenotypes of 187 F_2 plants from TX303×CO159 (Edwards et al., 1992). Four of 12 marker loci associated with GY variation also were associated with EL. These marker loci also were associated with other yield components, such as KRN and ENP.

Beavis et al. (1994) genotyped 112 $F_{2:4}$ lines from the cross B73 × Mo17 at 96 RFLP loci and collected data from replicated trials on several agronomic traits to use in QTL analyses. They identified three to five QTL for GY and each of the yield components EL, ED, and KRN. The authors concluded that analysis of a small population of ≈ 100 progeny from a bi-parental cross could be used to detect real QTL.

Veldboom and Lee (1994) used 150 replicated $F_{2:3}$ lines and 103 RFLP loci to identify QTL for GY and yield components in a Mo17×H99 population. They identified five QTL for EL on five chromosomes. Only one genetic region was associated with GY, but it accounted for 35% of the trait's phenotypic variation: EL, ED, KD, and KWT also had significant genetic effects associated with the region. The level of dominance for EL, ED, and KRN ranged from partial dominance to over-dominance. A comparison of QTL from the investigation by Veldboom and Lee (1994) to QTL found by analysis of 186 replicated $F_{6:7}$ lines from Mo17×H99 at 101 RFLP loci was reported by Austin and Lee (1996). They reported that the use of $F_{6:7}$ lines allowed the detection of almost twice as many QTL than were found in the $F_{2:3}$ by Veldboom and Lee (1994). The authors reported finding six QTL for EL, five of which were unique to the $F_{6:7}$ generation. They speculated that some of the linked QTL for yield components found in the $F_{6:7}$ generation were detected as one QTL in the $F_{2:3}$ generation.

Veldboom and Lee (1996) compared QTL detection using simple interval mapping in stress (1990) and nonstress (1989) years at a single location using 150 $F_{2:3}$ lines from Mo17×H99. They reported that the genetic effects at QTL for GY and yield components identified in both environments had similar magnitudes and parental origin and were associated with the same marker loci. Their analysis of the mean environment detected three QTL for EL, one having dominant gene action and the others having over-dominant gene action. Five QTL were detected for ED, four for KD, seven for KWT, two for KRN and ENP, and one for GY. The authors also reported a unique region on chromosome 6 near *NPI280* that was associated with all traits evaluated.

Austin and Lee (1998) reported the evaluation of 185 $F_{6:7}$ lines from the Mo17×H99 population in stress (1993) and nonstress (1994) years at the same location used by Veldboom and Lee (1996). They used RFLP and SSR loci to map QTL. The researchers reported that only 9% of the yield component and GY QTL were identified in the stress, nonstress, and mean environment analyses. No EL QTL was detected in both the stress and nonstress environments. Data from the $F_{2:3}$ generation evaluated by Veldboom and Lee (1996) was reevaluated with an additive model using composite interval mapping and compared with the $F_{6:7}$ data collected by Austin and Lee (1998). More EL, ED, and KWT QTL were identified using data from the $F_{6:7}$ generation than from the $F_{2:3}$ generation. Validation of several of these QTL was provided by their identification in each generation.

Detection of QTL across two samples (evaluated in different environments) of 150 $F_{2:3}$ lines from Mo17×H99 was reported by Asmono (1998). Seventy-one QTL were identified for four traits: EL, KWT, ENP, and GY. Only 13 QTL were detected in both samples, four of which affected EL

variation. The author suggested that few QTL detected across samples was due to sampling variation and different environmental effects influencing each sample.

Populations and Methods for Mapping QTL

QTL are genetic regions associated with the phenotypic variation of quantitative traits. The effect of a QTL may be the result of a single gene, two linked genes, or a cluster of genes. The ability to identify, separate, and estimate QTL effects is dependent on the population structure, progeny types, sample size, and statistical techniques used to associate marker loci with phenotypic variation. Introductory material regarding the concepts of QTL mapping was provided by Falconer and Mackay (1996; their chapter 21). A brief review of progeny types, samples sizes, and the analyses for identifying QTL was provided by Lynch and Walsh (1998).

The identification of QTL may be completed within populations in which linkage disequilibrium was created between marker loci and QTL. A common procedure for creating linkage disequilibrium in plant species is by developing populations from the F_1 of inbred parents. Experimental populations such as F_2, backcross, recombinant inbred lines (RILs), doubled haploid lines (DHLs), and advanced intercross lines (AILs) are commonly used to identify and estimate the effects of QTL. Each population structure has unique advantages and disadvantages with regard to development time, genetic resolution, genetic effects estimated, and ability to maintain genotypes indefinitely. For the research presented in this dissertation, the F_2 population structure was used. The F_2 and F_2–derived lines may be associated with the same marker genotypes. The F_2–derived lines allow genotypes to be evaluated at several environments and often reduce the standard error of phenotype values. In addition, F_2 populations produce three genotypic classes that, with the use of co-dominant markers, allow the estimation of additive and dominance effects of QTL.

Statistical procedures for associating genetic regions with phenotypic variation have evolved from the single-factor analyses procedure used in initial QTL experiments (e.g., Thoday, 1961; Soller and Brody, 1976). The single-factor analysis concept remains the foundation of the more advanced QTL mapping techniques. Advanced QTL mapping techniques utilize genetic information from linkage maps (interval mapping; Lander and Botstein, 1989) to more accurately define the locations and effects of QTL.

For mapping QTL in this dissertation, the regression-based method (Haley and Knott, 1992) of composite interval mapping (CIM; Zeng, 1994; Jansen and Stam, 1994) was employed by the computer program PLABQTL version 1.1 (Utz and Melchinger, 1996). CIM uses the concepts of simple interval mapping (SIM; uses multiple regression) or interval mapping (IM; uses maximum likelihood) but increases the power to identify and characterize QTL, especially when multiple and

linked QTL are segregating in the population. Like IM and SIM, CIM tests for QTL within intervals, but has the advantage of accounting for the affects of linked and/or unlinked (i.e., genetic background variation) QTL. The addition of markers linked to QTL (cofactors) into the standard interval analysis can reduce the genetic background variation, increasing the power to detect QTL with smaller effects. The question of which and how many cofactors to include in the interval analysis has many solutions. A common procedure is to identify those markers associated with phenotypic variation and use them as cofactors (i.e., markers linked to QTL in other regions of genome, besides the interval being tested). The number of cofactors included in the model should be kept near the minimum needed to control the genetic background variation. Fitting too many or redundant markers tends to decrease power to detect QTL (Zeng, 1994) due to collinearity (correlation among marker loci used as cofactors), especially when samples sizes are small.

Detection of epistasis between QTL has received little attention compared with the detection of QTL with significant additive and dominance effects (main effects). QTL software, such as PLABQTL version 1.1 (Utz and Melchinger, 1996) and QTL Cartographer version1.6 (Basten et al. 2002), offers options to detect epistatic interactions between QTL with significant main effects. Estimating interactions between QTL with known main effects may increase the amount of phenotypic variation explained by a set of QTL, but greater interest lies in identifying QTL that have undetectable main effects with significant interactions. To identify such interactions, Holland et al. (1998) developed EPISTACY, a computer program to test all possible pairs of marker loci for significant interactions. Holland et al. (1997, 2002) identified epistatic interactions that had no significant main effects associated with both or one of the marker loci involved in the interaction. QTL identified only by their interaction may increase the amount of phenotypic variation explained by a set of QTL.

CHAPTER 2.
GENETIC ANALYSIS OF MAIZE EAR LENGTH

A paper to be submitted to *Crop Science*

Andrew J. Ross, Arnel R. Hallauer, Michael Lee, and Wendy L. Woodman-Clikeman

Abstract

The length of the maize (*Zea mays* L.) ear shoot can be a limiting factor for grain yield. The divergent sub-populations of the Iowa Long-Ear Synthetic (BSLE) differ in ear length by > 14 cm and provide a unique opportunity to investigate the inheritance of ear length (EL). This investigation was conducted to determine the number and effects of quantitative trait loci (QTL) affecting EL variation. Cupules per rank were estimated by the number of kernels in a 5-cm interval (K/5CM) of EL. A population developed by crossing inbreds derived from the long-ear and short-ear cycle 24 sub-populations of BSLE was used for this investigation. The genotypes of 188 F_2 plants were obtained at 160 marker loci. Each plant was self-pollinated and measured for EL and K/5CM. Phenotypes of the corresponding $F_{2:3}$ progeny were evaluated in eight replications balanced over four Iowa environments. QTL analysis was performed on F_2 and $F_{2:3}$ phenotypes. Nine QTL in the F_2 accounted for 54% of the EL variation, and 16 QTL in the $F_{2:3}$ accounted for 70%. The QTL on chromosome 6 accounted for 23% of EL variation in each generation. Five QTL for EL coincided between generations, and seven QTL corresponded to QTL from other populations. Twelve QTL were identified for K/5CM, but only one corresponded to an EL QTL. K/5CM *per se* provided little genetic or phenotypic explanatory value for understanding the EL phenotype.

Introduction

East (1911) used ear-length (EL) variation to illustrate that quantitative traits may be conditioned by many Mendelian factors (genes) that are independently inherited. Since East's illustration, EL has been thoroughly investigated through quantitative genetic theory and biometrics because of its positive correlation with grain yield. Biometry provides estimates of genetic effects that are cumulative for the entire genome, but cannot identify or estimate the effects of chromosomal regions that influence quantitative traits (Lamkey and Lee, 1993). Genetic studies aided by DNA markers have partitioned the maize genome into genetic intervals to estimate the number of loci and

allelic effects that influence quantitative traits. The inheritance of EL has been investigated by this procedure (Beavis et al., 1994; Veldboom and Lee, 1994, 1996; and Austin and Lee, 1996, 1998).

Beavis et al. (1994) genotyped 112 $F_{2:4}$ progeny from B73×Mo17 at 96 restriction fragment length polymorphisms (RFLP) loci and identified three QTL for EL from the mean of six replications of phenotypic data. Veldboom and Lee (1994) identified five QTL for EL when associations were made between 103 RFLP loci and the phenotypic data from two replications at one environment for 150 $F_{2:3}$ progeny of Mo17×H99. When these $F_{2:3}$ progeny were revaluated in a stress environment only two EL QTL were detected (Veldboom and Lee, 1996). The combined analysis of the two environments allowed three QTL to be identified (Veldboom and Lee, 1996). Austin and Lee (1996) detected six EL QTL from data of 186 replicated $F_{6:7}$ progeny of Mo17×H99 grown in two replications at one environment. The authors compared their results to those of Veldboom and Lee (1994) and found that five of the six QTL were unique to the $F_{6:7}$ generation. Austin and Lee (1998) evaluated 185 of the 186 $F_{6:7}$ lines in stress and nonstress years at the same location used by Veldboom and Lee (1996). Ten EL QTL were detected with mean phenotypic data of the two years, but no QTL were detected in both the stress and nonstress environments. Data from the $F_{2:3}$ generation evaluated by Veldboom and Lee (1996) were reevaluated with an additive model using composite interval mapping (CIM) and compared with the $F_{6:7}$ data collected by Austin and Lee (1998). Only one more EL QTL was identified using data from the $F_{6:7}$ generation compared with the $F_{2:3}$ generation. Three QTL were identified in both the $F_{2:3}$ and $F_{6:7}$ generations.

These studies used populations developed from crosses of elite inbreds that were developed for use in practical breeding applications. A population developed from parents with extreme phenotypes, especially those derived by divergent selection, should make it possible to increase the chances of identifying more loci that affect trait variation and by evaluating fewer individuals (Lander and Botstein, 1989; Falconer and Mackay, 1996). At Iowa State University, the Iowa Long-Ear Synthetic (BSLE) has undergone 30 cycles of divergent mass selection for EL. The long-ear and short-ear sub-populations differ in mean EL by > 14 cm and are diverse in plant and inflorescence traits (Lopez-Reynoso and Hallauer, 1998; Hallauer et al., 2003). The divergent sub-populations of BSLE provide a unique opportunity to study the inheritance of EL for the following reasons: 1) the synthetic was developed from 12 long-eared inbreds (Russell et al., 1971), which allowed for the accumulation of alleles that increase EL, 2) the 12 inbreds represent a broad spectrum of germplasm from the Corn Belt Dents, and 3) the divergence of EL was due to direct selection from a same base synthetic.

To study the inheritance of EL, a F_2 population was developed from inbreds derived from long-ear and short-ear BSLE cycle 24 sub-populations. Genotypes of 188 F_2 plants were associated with traits evaluated on plants *per se* and their corresponding $F_{2:3}$ progeny. EL was the primary trait under investigation and a second trait was a hypothesized component of EL, cupule number in a 5-cm interval of EL. The EL phenotype is the product of two main components, the number of cupules along the ear shoot (rachis), and the extension of the distance between cupules (i.e., internodes with cupules as nodes). These components are affected by environmental signals in both the vegetative and reproductive stages of plant development, and a stable EL phenotype is provided by the plant's ability to completely develop the ear shoot (i.e., allow all internodes to extend). Variation for EL may be partially explained by the variation of cupule number in a given interval of EL. Estimation of the number of cupules in a 5-cm interval of EL was completed by counting the kernels within the interval (each developed kernel in a row of kernels is attached to the rachis at a cupule); this trait was labeled K/5CM.

The objectives for the investigation were 1) to determine the genetic positions and effects of alleles associated with EL and K/5CM, 2) determine the genetic positions that have stable effects on EL and K/5CM variation across the F_2 and $F_{2:3}$ generations, 3) determine if K/5CM could be classified as a component of EL variation, and 4) compare genetic positions of EL and K/5CM to positions found in other populations.

Materials and Methods

Plant Materials

Germplasm for this investigation originated from the BSLE cycle 24 sub-populations. BSLE was developed by intermating 12 inbred lines that had above-average EL. The 12 inbreds were B50, B55, B56, B217*wx*, C103, N22A, N25, Oh29, W-17R-B, (B15/B18)-16, (Lancaster Comp.)-34, and (L317/187-2)-1-1-9 (Russell et al., 1971). Based on pedigree information of these inbreds, BSLE is comprised of approximately 34% Reid Yellow Dent (Reid, Funks, Osterland, and Iodent), 23% Lancaster Sure Crop, 13% Krug Yellow Dent, 4% Midland Yellow Dent, 4% Alph, 11% other open-pollinated varieties or breeding synthetics, and 11% undetermined germplasm. Mass selection for divergent EL was initiated in 1963 to select shorter ears in BSLE(M-S) and longer ears in BSLE(M-L). Hallauer et al. (2003) and Lopez-Reynoso and Hallauer (1998) provided details of selection in the two sub-populations.

For the investigation herein, 100 S_0 plants from each BSLE(M-L) C24 and BSLE(M-S) C24 were self-pollinated at the Agronomy and Agricultural Engineering Research Center (AAERC) near

Ames, IA, in 1990. The S_0 lines were subjected to the pedigree system of inbreeding with selection practiced among and within lines solely for increased [BSLE(M-L) C24] and decreased [BSLE(M-S) C24] EL from 1992 to1998 at the AAERC. The line BSLE(M-L)C24-37-1-1-1-1-1-1, designated LE-37, was the final selection for increased EL, and BSLE(M-S)C24-40-1-1-1-1-2-1, designated SE-40, was the final selection for decreased EL. The two inbred lines differ in EL by ≈ 14 cm and are diverse in ear and morphological traits.

Population Development & Phenotype Evaluation

Mating SE-40 with LE-37 at an off-season nursery in Hawaii, during January 1999, formed the bi-parental F_2 population. F_1 plants were self-pollinated at the AAERC during July 1999 and leaf tissue from each F_1 plant was obtained for DNA extraction. At the AAERC on 10 May 2000, 510 F_2 kernels from a single F_1 ear were hand-planted at a seeding rate of 2 kernels hill^{-1} in rows 5.5 m in length. Spacing between hills within a row was 0.30 m and between rows was 0.76 m. At the V4 growth stage (Ritchie et al., 1996), each hill was thinned to one F_2 plant. Four rows for each parent and their F_1 were planted at 5 d intervals (–5, 0, and +5) relative to planting the F_2 kernels and were maintained with the F_2 rows. The parent and F_1 plants served as a homogenous genetic source to estimate variation due to environment.

Three leaves from each F_2 plant and a bulk of leaves from 25 plants for each parent were harvested, for DNA extraction, during V7. Each F_2 plant was self-pollinated for three consecutive days after reaching the climax of male anthesis. This procedure was implemented to avoid biasing ear length due to unpollinated spikelets on the terminal end of the rachis. Cumulative growing degree days (°C) were determined for each F_2 plant from planting until female anthesis. At maturity, all ears on each competitive F_2 plant were hand-harvested, dried, and the primary self-pollinated ear measured for EL and K/5CM. EL was measured from the base to the terminal end of the rachis and recorded in centimeters. K/5CM was obtained by counting the number of kernels in a 5-cm interval at the middle of the ear. Data from 120 open-pollinated plants (40 from each planting interval) of each parent and their F_1 were also collected.

A random sample of 189 F_2 plants was taken from the population and evaluated in replicated-progeny rows in 2001. The 189 $F_{2:3}$ progeny and 11 other entries [three entries each of LE-37, SE-40, and SE-40×LE-37, and one entry each of (SE-40×LE-37)×SE-40 and (SE-40×LE-37)×LE-37] were randomized to single-row plots of a 10×20 row-column lattice experiment. The experiment was evaluated in two replications near Ames, Ankeny, Crawfordsville, and Lewis, IA. Plots were 5.5 m in length and 0.76 m separated adjacent plots. Plots were machine planted at Ames on 26 April, Crawfordsville on 02 May, and Lewis on 27 April 2001 at a seeding rate of 30 kernels plot^{-1} (71 700

kernels ha^{-1}) and hand-planted at Ankeny on 15 May 2001 at a rate of 2 kernels $hill^{-1}$ with 15 hills $plot^{-1}$. Plots were thinned at V5–V7 to 15 plants $plot^{-1}$ (35 900 plants ha^{-1}). This plant density was used for evaluation of F_2 plants in 2000, and was maintained across the F_2 and $F_{2:3}$ generations to minimize environmental variation. The cumulative growing degree days (°C) from planting until 50% of the plants within a plot reached female anthesis were recorded at Ames, IA. At maturity, the primary ear from the first 10 competitive plants per plot was hand-harvested and dried at 38 C for 4 d. The plot mean for EL was obtained by measuring 10 ears and for K/5CM by counting kernels on five ears with good kernel development.

Phenotype Analysis

Phenotype data were analyzed from the F_2 and $F_{2:3}$ generations. One F_2 and its progeny were excluded from all analyses because data on cob color (*P1* locus) were not consistent across generations, indicating that the F_2 plant was not self-pollinated. For data analysis in the F_2, the mean and variance were computed for each trait within each source of plants (SE-40, LE-37, F_1, and F_2) grown in 2000. The variance from each source of plants was used to calculate broad-sense heritabilities (h^2) on a plant basis as described by Weber and Moorthy (1952).

Plot means of each trait were used for data analysis in the $F_{2:3}$ generation. The plot means at each environment were adjusted for intrablock effects from a lattice analysis that included rows and columns as random sources of variation. The adjusted least-square means from each environment were used in the analysis of data combined across environments (mean environment). The combined analysis was performed using a general linear model with environments, entries, and their interaction considered random sources of variation. For each trait, the sums of squares for entries and entries × environment were partitioned into among $F_{2:3}$ progeny, among checks, and the orthogonal contrast. *F*-tests were used to determine the significance of each source of variation.

Sources of variation due to the $F_{2:3}$ progeny and the $F_{2:3}$ progeny×environment interaction were used in calculating h^2, variance components, and phenotypic correlation coefficients. Heritability on a progeny-mean basis and its 95%-confidence interval were computed according to Knapp et al. (1985). Heritability also was estimated by regressing $F_{2:3}$–progeny means onto F_2 plant values. Phenotypic correlation coefficients between EL, K/5CM, and growing degree days to female anthesis within each generation were computed.

Genetic Map

DNA was extracted from lyophilized leaf tissue harvested from the F_1 plant in 2000 and from individual F_2 plants and a group of 25 plants for each parent grown in 2001. DNA extraction was completed using a modified-CTAB protocol (Saghai-Maroof et al., 1984). The genetic linkage map

was developed from 188 F_2 plants and 160 co-dominant marker loci; 96 simple sequence repeat (SSR) and 62 RFLP loci, one haplotype locus (u11011573), and the *P1* locus. To distinguish between types of marker loci, hereafter, SSR loci will be written in lowercase type and RFLP loci in uppercase type. Methods followed for data collection on SSR loci were according to Senior et al. (1996) and for RFLP loci according to Veldboom et al. (1994). A chi-square goodness-of-fit test was computed for each locus with the expected segregation ratio of 1:2:1.

Primer sequences for the SSR loci are available from the Maize Database (http://www.agron.missouri.edu/ssr.html; verified 09/16/02) except for *tb1isussr* that amplifies a di-nucleotide repeat within the DNA sequence of the teosinte branched gene (*tb1*) (Wang et al., 1999; Genbank accession AF131659) and *un5* that amplifies an imperfect repeat. Both SSR loci were developed at Iowa State University and have the following forward (F) and reverse (R) primer sequences: *tb1isussr*, F-tgcatagagaggtggtatgatc R-aggtcctggcactaagagcagt; and *un5*, F-cacgccaagaagttcactca R-tattgacggcgacgactgat. The haplotype locus *u11011573* on chromosome 4 was formed from two SSR loci, *umc1101* and *umc1573*, that gave dominant banding patterns for SE-40 and LE-37, respectively, and were not separated by recombination. This locus was developed because no co-dominant loci were identified that would reduce an interval > 45 cM on the long arm of chromosome 4.

The genetic map was compiled using MAPMAKER/EXP 3.0 (Lander et al., 1987). Marker loci were assigned to linkage groups by the "group" command using the default criteria of a maximum likelihood of odds (LOD) score of 3.0 and a minimum distance of 50 Haldane centimorgans (cM) for declaring loci genetically linked. The "order" command was used to determine the arrangement of loci within linkage groups. Output from MAPMAKER/EXP using the "error detection on" and "genotype" commands was manually checked for erroneous recombination data. The MAPMAKER program was iterated five times and the "ripple" command was employed to ensure an accurate and stable order of loci was obtained.

Genetic Analysis

Detection of QTL was completed using the regression-based method (Haley and Knott, 1992) of composite interval mapping (CIM; Zeng, 1994; Jansen, 1993) employed by the computer program PLABQTL version 1.1 (Utz and Melchinger, 1996). The analysis was completed using a series of PLABQTL runs similar to the procedure described by Holland et al. (2002). The initial run was completed with the "cov sel" command that selected cofactors (marker loci) using stepwise regression with the program's default *F*-to-enter (to-drop) threshold of 3.5. The second run was done by setting all marker loci as cofactors ("cov/+sel" command) that may allow linked QTL with opposite effects

to be resolved. The marker loci closest to each detected QTL in the initial or second runs were used as cofactors in a third run. If new QTL were detected in this run, they were fitted in a following run. This procedure was continued until no new QTL were detected. As suggested by Holland et al. (2002), if different QTL were detected in the series of runs, subsets of these QTL were tested. A model stipulated by cofactors being linked to QTL (Zeng, 1994) with significant ($P < 0.05$) genetic effects and having the lowest Akaike's information criterion (Jansen, 1993) was chosen as the final multiple-QTL model. To determine the amount of phenotypic variation that a defined group of QTL may explain, the "seq" statement was used. QTL of interest were deleted from the final multiple-QTL model and the remaining QTL were used as regressors. The difference between the coefficient of multiple determination (R^2) between the full and reduced-models was considered the amount of phenotypic variation that the deleted-QTL group explained.

The LOD threshold for declaring the presence of QTL was 2.5. This threshold is the default value of PLABQTL and was in the range of thresholds commonly used in QTL experiments (Lander & Botstein, 1989; Krakowsky et al., 2002). The authors acknowledge the threshold was liberal and increased the probability of type I errors. However, a LOD of 2.5 was greater than the LOD of 2.0 used in previous studies (Beavis et al., 1994; Veldboom and Lee, 1994, 1996; Austin and Lee, 1998) to identify QTL for EL. For reference, permutation tests ($n = 1000$; Churchill and Doerge, 1994) for EL and K/5CM measured in each generation (F_2 plants and $F_{2:3}$–progeny) indicated that a comparison-wise threshold of LOD ≈ 4.0 was necessary to maintain an experiment-wise significance level of $\alpha = 0.05$.

Digenic epistasis was estimated between all possible pairs of marker loci using EPISTACY (Holland, 1998). A comparison-wise threshold of $P < 0.00026$ was used to declare interactions significant. This threshold was a liberal Bonferroni-style significance level computed by assuming each of the 20 chromosome arms was an independent group ($n = 190$). Individual interaction terms were added to a multiple-regression model with marker loci nearest each QTL detected by PLABQTL. Interaction terms that remained significant ($P < 0.05$) in the regression model and increased the adjusted-R^2 of the model were considered important for a trait's heredity.

QTL were defined as 20-cM interval placed symmetrically on the highest LOD value for each region. A 20-cM interval was used instead of the one-LOD support interval proposed by Lander and Botstein (1989) because one-LOD support intervals are often underestimated (Visscher et al., 1996), and mapping resolution is low in F_2–derived mapping populations. Additional rationale for use of the 20-cM interval for defining the bounds of QTL was provided by Cardinal et al. (2001). The additive effect (a) and dominance deviation (d) were calculated for each QTL (Falconer and Mackay, 1996).

Gene action was assigned to each QTL based on the level of dominance and the criteria defined by Stuber et al. (1987): additive (A) = 0–0.20; partial-dominance (PD) = 0.21–0.80; dominance (D) = 0.81–1.20; and over-dominance (OD) > 1.21. The level of dominance for F_2 plants was defined as d/a and for $F_{2:3}$ progeny as $2d/a$. The ratios differ between generations because at a given locus only half of the $F_{2:3}$ plants would exhibit dominance; therefore, the dominance effect was doubled for determining gene action. The phenotypic variation explained by the genetic effects (a or d) at each QTL was estimated with a partial r^2 value computed by dividing the partial sums of squares for each effect by the total sums of squares for the regression model (Holland et al., 1997, 2002). Partial r^2 values computed in this manner will not sum to more than the adjusted-R^2 for the multiple-QTL model, unlike partial r^2 values computed by PLABQTL (Holland et al., 2002).

QTL analysis was completed on five sets of phenotypic data for each trait: F_2–plant values, adjusted-$F_{2:3}$–progeny means from each of four environments, and entry means from the $F_{2:3}$ mean environment. To determine if QTL were identified in different analyses, the map positions of QTL were compared. If QTL (20-cM interval) overlapped, the QTL were considered identical. To compare the location of QTL identified in the SE-40×LE-37 population evaluated herein to QTL found in other populations, a 20-cM interval redefined the boundaries of QTL in other populations and comparisons were aided with the linkage to common marker loci.

Results

Phenotype Analysis

SE-40 and LE-37 each had EI means that were nearly identical when evaluated on a plant-basis at Ames in 2000 and on entry-mean basis in 2001 (Table 1). The difference between the parents was ≈ 14 cm. The F_1 in 2000 had a mean EL equivalent to LE-37 and significantly greater than LE-37 in 2001. The change in EL for the F_1 may be due to the experimental design used in 2000 and 2001. The F_1 and parent plants in 2000 were each planted in four-row blocks, but in 2001 the plant types were planted as single-row plots randomized among entries that were mostly $F_{2:3}$ progeny that had less vigorous (coefficient of inbreeding = 0.5) growth patterns, providing F_1 entries a competitive advantage. K/5CM was also extreme between the two parents and the means across years maintained their relative magnitudes.

The range of EL among F_2 plants (13 cm) and $F_{2:3}$ progeny (7 cm) from SE-40×LE-37 indicated variability in this population that should aid in the identification of QTL. Only three F_2 plants had EL greater than LE-37 and there were no transgressive $F_{2:3}$ progeny. The range of EL in the $F_{2:3}$ was 7 cm less than the difference between the two parents, and illustrated the effect of smaller

sample sizes ($n < 500$; Beavis, 1998) by the underrepresentation of potential genotypes, especially parental types. Heritability on an progeny-mean basis was 0.94 for EL and 0.83 for K/5CM, suggesting significant genetic variation among $F_{2:3}$ progeny and/or that phenotypes were stable across environments. Environments were significantly different for each trait, but there was no $F_{2:3}$–progeny×environment interaction. Heritabilities estimated on a single-plant basis and by F_2–$F_{2:3}$ regression were smaller than entry-mean estimates, but the magnitude of these estimates was relatively similar between EL and K/5CM for the two estimation methods (Table 1).

Phenotypic correlation coefficients (r_ps) between EL and K/5CM were negative and significant ($P < 0.01$) among F_2 plants ($r_p = -0.26$), and $F_{2:3}$–progeny means ($r_p = -0.22$). However, the r_ps were relatively low and despite statistical significance, K/5CM may not characterize EL well. A negative correlation ($r_p = -0.26$) existed between female anthesis and EL in the F_2 generation but not among $F_{2:3}$–progeny means. In contrast, no correlation was present between female anthesis and K/5CM in the F_2 generation, but was negative ($r_p = -0.37$) among $F_{2:3}$–progeny means. The inconsistency of the r_ps across generations and their low values indicated that EL and K/5CM were not greatly influenced by the length of the plants' vegetative stage.

Genetic Map

The SE-40×LE-37 genetic map was developed from 188 F_2 plants genotyped at 160 co-dominant loci, and consisted of 10 linkage groups corresponding to the 10 maize chromosomes. The map had a cumulative distance of 1662 cM, and interval distances between loci ranged from 1 to 29 cM with a median interval distance of 10 cM. Genotypic data were nearly complete with < 0.5% missing data. Marker alleles represented an equal genome contribution from each parent with SE-40 contributing only 4% more alleles than LE-37. The expected segregation ratio of 1:2:1 for co-dominant marker alleles was met ($P > 0.01$), as confirmed by a chi-square goodness-of-fit test, for all loci except *bnlg1006* and *umc1040* on chromosomes 5 and 9, respectively.

Genetic Analysis

Nine EL QTL and three K/5CM QTL were detected in the F_2. Sixteen QTL were detected for EL and 12 for K/5CM from the mean environment of the $F_{2:3}$. The number of QTL detected for each trait in the F_2 and $F_{2:3}$ environments is summarized in Table 2. A similar number of QTL for EL was detected among the four environments used to evaluate the $F_{2:3}$ and a similar portion of phenotypic variance was explained by the QTL at each environment (Table 2). Only 3 of 4 environments were similar in QTL identification for K/5CM. Silk-feeding by corn rootworm beetles (*Diabrotica*) may have caused reduced pollination and kernel development on progenies at the Lewis environment, leading to sub-average QTL detection.

Detection of QTL in the mean environment was representative of the four environments. An average of 75% of the EL QTL and 70% of the K/5CM QTL from individual environments were also identified in the mean environment. Because of the consistent detection of QTL, the mean environment was the focus of further discussion regarding the $F_{2:3}$ and used to compare QTL positions across generations and other populations. The mean environment also allows for additional QTL with smaller effects to be detected (Austin and Lee, 1998). Three EL QTL and one K/5CM QTL were not identified at individual environments, but were detected in the mean environment. Two of the EL QTL only affected EL by a dominance effect. The third QTL increased EL by an additive effect with the favorable allele originating from SE-40.

EL QTL were identified on chromosomes 1, 2, 3, 5, 6, and 9 and explained 54% of the phenotypic variation among F_2 plants (Table 3 and Figure 1). The 16 QTL in the $F_{2:3}$ were located on every chromosome except 8 and 10, and explained 70% of the EL variation. A region on chromosome 9 was detected where two QTL that affect $F_{2:3}$–progeny EL overlap by 8 cM. Based on the criterion for this investigation the QTL should have been classified as one locus, but the genetic effects of these loci differed and warranted an exemption from the criterion. The QTL near *phi022* had a dominance effect of 0.6 cm with no additive effect, whereas the QTL near *umc1691* had an additive effect of 0.7 cm.

Alleles from LE-37 increased EL at all QTL except one locus in the F_2 and three loci in the $F_{2:3}$. The predominant genetic effect at QTL was additive, though dominance effects were also significant at ≈ 40% of these loci. QTL with the largest additive effects ($a \geq 0.6$) were located on chromosomes 5, 6, and 9, in the F_2 and on 3, 5, 6, and 9 in the $F_{2:3}$. QTL near *UMC78* on chromosome 2 and *phi022* on chromosome 9 in the $F_{2:3}$ only showed dominance effects. Gene action of loci in both generations was variable with half of the loci having additive or partial-dominance gene effects and the remaining loci had dominance or over-dominance effects. Chromosome 6 had the greatest affect on EL variation. Two QTL in the F_2 and three QTL in the $F_{2:3}$ accounted for 23% of the phenotypic variation in each generation. In addition, the three QTL on chromosome 6 were detected at all environments in the $F_{2:3}$ and showed stable additive effects (data not shown).

Five QTL on chromosomes 1, 2, 3, 6, and 9 identified in the F_2 were also detected in the $F_{2:3}$ (Table 3; Figure 1). QTL on chromosomes 3 and 6 seemed to have the most stability across generations. A strong additive effect ($a \approx 1.0$ for F_2 and $a = 0.7$ for $F_{2:3}$) for increased EL was attributed to the LE-37 alleles at these QTL in both generations. The QTL on chromosome 6 (*UMC160A*) in the F_2 possibly represented two QTL detected in the $F_{2:3}$ (see Figure 1). The LE-37 alleles on chromosomes 1 and 2 also increased EL in both generations, but the magnitude of the

genetic effects was not as stable as those QTL on chromosomes 3 and 6. The QTL on chromosome 9 did not have stable genetic effects across generations. The instability at this region may be a consequence of two or more EL QTL with different genetic effects and/or parental origin of alleles that increase EL. This explanation receives support from the presence of two QTL detected in the $F_{2:3}$ with different genetic effects, and visual observation of likelihood plots from CIM. A region (*bnlg105–umc1019*) on chromosome 5 was not considered to have QTL that coincided across generations, but did provide evidence for more than one QTL in relatively close proximity between generations. A QTL with an allele from SE-40 increased EL in the F_2, and was flanked by two QTL from the $F_{2:3}$ with LE-37 alleles increasing EL, indicating more than two QTL were present at this region (Table 3; Figure 1).

The number of QTL identified for K/5CM was less than detected for EL. Three QTL on chromosomes 1, 5, and 9 in the F_2 explained ≈ 25% of the K/5CM variation. Twelve QTL, on every chromosome except chromosome 4, explained ≈ 60% of the K/5CM variation. All QTL except for the locus on chromosome 7 (*BNL14.07*) increased K/5CM by an additive effect. Dominance effects were present at half of these loci. K/5CM was increased by an allele from SE-40 at most of the QTL, and could be interpreted as a decrease in average internode length (average distance between cupules) in this 5-cm interval. The allele with the largest affect ($a = 0.7$ kernels) on K/CM in the F_2 originated from LE-37. Half the K/5CM QTL had additive to partial-dominance gene action. Five K/5CM QTL were detected at ≥ 75% of the $F_{2:3}$ environments and showed stable additive effects. Only one QTL, however, coincided between generations. On chromosome 9 (*NPI567–phi022*) an allele from SE-40 consistently increased the number of kernels by additive effects, but the dominance effect was variable across generations (Table 3, Figure 1).

Digenic epistasis was identified for EL and K/5CM in each generation, using EPISTACY. However, the epistatic interactions for EL either did not remain significant or account for additional EL variation when incorporated into a multiple main-effect QTL model. Three digenic interactions explained additional K/5CM variation when added to the multiple main-effect QTL models. The additive × additive (*a*×*a*) interaction of these loci (*phi021* and *bnlg2291*) on chromosome 4 and the *a*×*a* and dominant × dominant interaction between loci on chromosomes 6 (*phi452693*) and 8 (*ISU91*) cumulatively improved the multiple-QTL model by explaining an additional 8% of the K/5CM variation among F_2 plants. A dominant (*bnlg602*, chromosome 3) × additive (*phi034*, chromosome 7) interaction identified in the $F_{2:3}$ explained an additional 2% of the K/5CM variation.

Discussion

This investigation identified nine EL QTL in the F_2 and 16 in the $F_{2:3}$ generations. Other studies have not identified this many EL QTL in a single population (Stuber et al., 1987; Abler et al. 1991; Beavis et al. 1994; Veldboom and Lee, 1994, 1996; Austin and Lee, 1996, 1998). From previous studies, Austin and Lee (1998) had detected the most EL QTL (10) by using replicated $F_{6:7}$ progeny of Mo17×H99, a well structured genetic map, and CIM.

There are several possible explanations for the increased number of EL QTL identified in SE-40×LE-37: 1) the accumulation of alleles for increased EL in BSLE increased the probability of having large effects at individual loci; 2) the divergence of alleles for increased EL into LE-37 and alleles for decreased EL into SE-40 may have decreased the probability that alleles of opposite effects would be linked in repulsion causing a cancellation or reduction of their effects; 3) the high heritability (0.94) of EL resulting from precise estimates of phenotypes at four environments and the lack of genotype × environment interactions increased the power to detect QTL (Knapp and Bridges, 1990); and 4) a genetic map with well dispersed marker loci and < 0.5% absent data aided QTL detection by CIM. None of these explanations should be considered the primary reason for the increased number of QTL observed because QTL identification was a result of their cumulative effects.

Though 16 QTL for EL in the $F_{2:3}$ were detected, the actual number of QTL was probably not determined. The average EL of SE-40 was 8 cm indicating that some QTL for EL remained fixed between the two parents, eluding detection in this population. Three QTL that increased EL in the $F_{2:3}$ originated from SE-40. However, their combined effect would not explain the presence of 8 cm of EL. The number of progeny evaluated in this study also hindered the detection of QTL because it did not take full advantage of the potential genetic variance.

Epistasis and EL Heredity

The additive and dominance effects of the EL QTL accounted for 75% of genotypic variation (phenotypic variation / h^2) among $F_{2:3}$–progeny means, leaving only 25% of the genotypic variation to be attributed to unidentified main-effects and epistatic effects. The failure of epistatic interactions to account for additional EL variation, when added to the multiple-QTL model, was also hindered by the relatively small sample (n = 188) of genotypes used for QTL identification. The lack of transgressive segregates and the condensed range of EL means among the $F_{2:3}$ progeny indicated this sample size was not adequate to represent the true distribution of EL genotypes. The inability of epistasis to explain additional variation, however, should not be considered as evidence that epistasis is not important for the heredity of EL. Incorporating epistatic interactions into a QTL model that has 16

main-effect loci may be unrealistic and rarely encountered in practical breeding applications. Seldom would a breeding population exist in which so many alleles that increase EL segregate simultaneously. If some alleles in this population were fixed from segregating, interactions between loci may have accounted for a portion of the phenotypic variation. Russell and Eberhart (1970) and Russell (1971) used near isogenic lines (NILs) and found that epistasis significantly affected EL variation. In addition, studies using biometrical techniques detect epistatic effects as an important source of variation for EL among elite-inbred crosses (Gamble, 1962; Darrah and Hallauer, 1972; Wolf and Hallauer, 1997).

Though epistatic interactions did not improve the multiple-QTL model, the effect of two interactions remained quite impressive. The interaction effects on EL were detected in the mean environment and all four individual environments used to evaluate the $F_{2:3}$ progeny. A *d×a* interaction resulted when the region on chromosome 7 (*un5–phi034*) was heterozygous and disrupted the additive (linear) effect of alleles from the distal region of chromosome 5 (*bnlg1306*) (Figure 2a). The deviation caused the LE-37 homozygote and the heterozygote genotypes at *bnlg1306* to become under-dominant by ≈ 0.5 cm and the SE-40 homozygote to be over-dominant by ≈ 2 cm. The second interaction involved the QTL on chromosome 4 (*umc1194*) where the EL increase was provided by an allele from SE-40. The additive effect at this QTL was affected by the heterozygote at a region on chromosome 10 marked by *bnlg2190* (Figure 2b). The LE-37 homozygote that decreased EL became over-dominant by ≈ 1.5 cm and SE-40 homozygote, which increased EL, was under-dominant by ≈ 1.5 cm when *bnlg2190* was heterozygous. These interactions provide illustrations of epistasis that distorts the phenotypic values expected from an inheritance model that excludes epistasis. Further study of these interactions in controlled genetic backgrounds (i.e., NILs) would help estimate the true impact of epistatic gene effects on EL inheritance.

Generation Affect on QTL Detection

Eleven EL QTL identified in the $F_{2:3}$ were not detected in the F_2. QTL detection in each generation should not have been affected by the genetic information, because individuals, marker loci, and recombination data were the same. The difference in QTL detection was attributed to the phenotype estimates of each generation. Phenotypes on F_2 plants were estimated from a single measurement, but $F_{2:3}$–progeny means represented measurements of 80 F_3 plants for EL and 40 plants for K/5CM. Knapp and Bridges (1990) addressed the issue of unreplicated and replicated progeny and illustrated how replication increased the power to detect QTL.

Progeny replication also affected the estimates of genetic effects, as the average effect in the F_2 was larger than in the $F_{2:3}$ (Table 3). Sample size (Beavis, 1998), genetic recombination, genotype

× environment interactions, and the underestimation of epistasis (Lee, 1995) are known to bias estimates of QTL effects. The genetic information, however, was the same for both generations, and genotype × environment interactions may not be a plausible explanation because the parents and F_1 had relatively stable phenotypes across years (EL means in Table 1). One factor for explaining the difference of effects is the difference of phenotype means and variances between generations. The mean difference was 2 cm for EL and one kernel for K/5CM, and the range of the F_2 plants was 6 cm (85%) larger than the range of EL phenotypes in the $F_{2:3}$. To adjust for the difference in trait variances, each effect was standardized by dividing the effect by the standard deviation specific for its' generation and trait (data not shown; Morris et al., 1999). The average significant additive effect in standard deviation units was equal between generations for EL. The average difference of effects between generations was reduced by 50% for the additive effects of K/5CM and 75% for the dominance effects of EL when effects were standardized. Dominance effects of K/5CM did not benefit from standardization. Differences in the magnitude of effects across generations were also possible because the generations were at different levels of inbreeding, and only half of the $F_{2:3}$ progeny would exhibit dominance compared with its heterozygous F_2 "parent."

QTL Validation

Confidence that QTL were not falsely identified was increased for most QTL because they were detected in different environments, generations, and other populations. In this study, seven EL QTL and five K/5CM QTL were identified in ≥ 75% of the $F_{2:3}$ environments and five EL QTL and one K/5CM QTL coincided between generations. Validation of QTL by comparing across populations was limited because of the progeny type and number, genetic maps, and statistical techniques used to define QTL in other populations. Many of the populations had genetic maps with sparse marker loci that were not shared by SE-40×LE-37 and used analysis techniques, such as single-factor ANOVA or interval mapping, that resulted in vague QTL boundaries. Austin and Lee (1998) used CIM to identify QTL affecting EL in the $F_{2:3}$ and $F_{6:7}$ progeny of Mo17×H99. The SE-40×LE-37 population had 32 marker loci in common with the Mo17×H99 genetic map. For this reason, these two populations served as the main comparison for EL QTL.

Seven EL QTL were common between the SE-40×LE-37 (SL) $F_{2:3}$ and Mo17×H99 (MH) $F_{2:3}$ or $F_{6:7}$ generations. The three QTL on chromosome 1 of the SL $F_{2:3}$ coincided with QTL in the $F_{2:3}$ of MH. The two most proximal QTL were also identified from $F_{2:4}$ progeny of a B73×Mo17 population (Beavis et al. 1994). A QTL on chromosome 5 (*BNL5.02*) was identified in both generations of SL and the $F_{2:3}$ of MH. A QTL (near *UMC160A*) identified on chromosome 6 in the SL F_2 that probably represented two QTL in the SL $F_{2:3}$ was identified in the MH $F_{2:3}$ as one QTL and in the MH $F_{6:7}$ as

two QTL. The two QTL (marked by *nc013* and *bnlg1740*) found in the SL $F_{2:3}$ and the MH $F_{6:7}$ also coincided, providing additional confidence that there are at least two QTL in this region. The QTL for both EL and K/5CM on chromosome 9 found in each generation of SL may correspond to a QTL from the $F_{6:7}$ of MH and a QTL identified by Beavis et al. (1994) in B73×Mo17.

The trait K/5CM was used as an estimate for the number of cupules in 5 cm of EL. QTL for the number of cupules per row were identified in two teosinte×maize populations (Doebley et al., 1990; Doebley and Stec, 1991, 1993). QTL identified in the teosinte×maize populations seemed to be near QTL for K/5CM or EL. The primary examples were on chromosome 1 where the EL QTL (*NPI234*) and the K/5CM QTL (*ISU6*) from the $F_{2:3}$ of SL coincided with the two largest QTL for cupule number in each teosinte×maize population.

The consistent detection of QTL across environments, generations, and/or other populations concomitantly provides assurance of QTL existence and importance of allelic differences in different genetic and environmental backgrounds for the heredity of EL and K/5CM. QTL from the $F_{2:3}$ of SE-40×LE-37 were reliable estimates of QTL locations and effects, and additional confidence was gained by identifying these QTL in other populations. A population for an adequate comparison may not yet exist however as ≈ 40% more EL QTL were detected in the $F_{2:3}$ generation of SE-40×LE-37 than the largest number of QTL previously reported (Austin and Lee, 1998). Evaluation of recombinant inbred lines derived from these $F_{2:3}$ progeny may provide data for a more appropriate validation of these QTL.

Relation of EL with K/5CM

Results from the QTL comparison between EL and K/5CM did not support the hypothesis that K/5CM is a descriptive component of EL variation. Twelve QTL in the SE-40×LE-37 $F_{2:3}$ affected K/5CM, but only the QTL on chromosome 9 coincided with an EL QTL. This region also had coinciding QTL for EL and K/5CM in the F_2. The QTL at this region affected EL through different genetic effects in the $F_{2:3}$ but in general an increase of EL and a decrease in K/5CM was due to an allele(s) from LE-37 in both generations. The low phenotypic correlation indicated that QTL for these traits might not coincide. From the correlation coefficient, it was estimated that K/5CM only explained 5% of the EL variation among $F_{2:3}$ progeny. Additionally, components of complex traits have higher heritabilities than the trait being partitioned (Hallauer and Miranda, 1988), and this was not the case for K/5CM, which had a lower heritability than EL. The conclusion of these results was that K/5CM should not be considered a component of EL, as it lacked phenotypic and genetic explanatory value.

The failure of K/5CM *per se* to assist in understanding the EL phenotype is not an indication that cupules per 5 cm would be a poor explanatory component of EL. It is likely that K/5CM was a poor estimate of cupules per 5 cm, and a method not dependent on ovule fertilization and kernel development should have been used to determine cupule number. A more precise estimate of cupule number may yield a different understanding of the relationship between cupule number, distance between cupules, and EL.

Although, it is probable that the distance between cupules and cupule number, as measured in this study (at the middle of the ear), have less impact on the final EL than the ability of the ear shoot to completely develop (i.e., allow all internodes to extend). SE-40 has an ear shoot that never fully develops, leaving a kernel-less terminal. Contrarily, ear shoots of LE-37 routinely extend until the tip of the rachis can be observed as a sharp tip. This lack of and complete ear-shoot development can also be observed in the short-ear and long-ear sub-populations of BSLE, respectively. The allelic differences at genes that provide the ability for complete shoot development are probably the primary cause for much of the EL variation.

Herein, QTL were identified from progeny grown in relatively "stress-free" environments that should not have significantly inhibited ear shoot extension and complete development. These environments were provided by allowing plants to develop under a plant density of 35,900 plants ha^{-1}, when most commercial plantings are twice as dense. The general stability of allelic effects observed at QTL identified herein may differ, and additional QTL may be detected, when these progeny are introduced to environmental stresses. The stability of alleles that control EL under different plant densities may provide further understanding of the role EL has in limiting grain yield.

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Table 1. Means, ranges, and broad-sense heritabilities (h^2) for EL and K/5CM of maize evaluated on the parents and generations of SE-40×LE-37 in 2000 and 2001.

	EL		K/5CM	
Parent or generation	$\bar{x}$ ± SE †	Range	$\bar{x}$ ± SE	Range
2000 (plant basis)	cm		no.	
SE-40	8.3 ± 0.1	5.1–11.8	12.1 ± 0.1	9–15
LE-37	22.5 ± 0.2	17.1–27.0	9.3 ± 0.3	8–10
F_1	22.1 ± 0.1	18.6–24.4	11.8 ± 0.1	10–13
F_2 (188 plants)	18.8 ± 0.2	11.1–23.9	12.0 ± 0.1	9–17
h^2 ‡	0.65		0.48	
2001 (entry-mean basis)				
SE-40	8.2 ± 0.2	–	10.5 ± 0.2	–
LE-37	21.9 ± 0.2	–	7.1 ± 0.2	–
F_1	23.1 ± 0.2	–	11.2 ± 0.2	–
$F_{2:3}$ (188 lines)	17.0 ± 0.0 §	12.9–19.8	11.0 ± 0.0	6.8–13.9
h^2 [CI] ¶	0.94 [0.93–0.95]		0.83 [0.78–0.86]	
σ_g^2 ± SE	2.0 ± 0.2		0.6 ± 0.0	
σ_{ge}^2 ± SE	0.5 ± 0.0		0.5 ± 0.0	
F_2–$F_{2:3}$ regression				
h^2 [CI] #	0.37 [0.30–0.44]		0.24 [0.14–0.34]	

† Means and standard errors (SE) estimated from ≈120 plants of SE-40, LE-37, and their F_1 in 2000, and triplicate entries in 2001.

‡ h^2 on plant basis (Weber and Moorthy, 1952).

§ SE of zero was due to rounding.

¶ h^2 and 95%-confidence interval [CI] on progeny-mean basis (Knapp et al., 1985).

h^2 and 95%-CI estimated from linear regression of $F_{2:3}$–progeny means onto F_2 plants.

Table 2. Summary of QTL analyses for EL and K/5CM in maize for each generation-environment combination of SE-40×LE-37 progeny.

Generation (Gen.) & Environment (Env.)	EL QTL detected				K/5CM QTL detected			
	Total	Unique to Gen./Env. †	In $F_{2:3}$ Mean Env. ‡	σ_p^2 explained §	Total	Unique to Gen./Env.	In $F_{2:3}$ Mean Env.	σ_p^2 explained
	no.			%	no.			%
F_2 AAERC (Ames)	9	3	5	54	3	2	1	26
$F_{2:3}$ Ames	11	2	6	62	9	0	7	52
$F_{2:3}$ Ankeny	14	4	10	60	10	2	7	48
$F_{2:3}$ Crawfordsville	12	0	10	58	11	0	8	48
$F_{2:3}$ Lewis	10	1	9	54	5	1	3	27
$F_{2:3}$ Mean	16	1	--	70	12	1	--	62

† Number of QTL identified solely in the generation-environment combination.

‡ Number of QTL identified in the analysis of the given generation-environment combination and also in the $F_{2:3}$–progeny mean environment.

§ Phenotypic variation explained by the multiple-QTL model adjusted for degrees of freedom.

Table 3. Summary of QTL positions, genetic effects, and consistency (†) of detection between $F_{2:3}$ progeny and their "parental" F_2 plants in the SE-40×LE-37 maize population.

	$F_{2:3}$ Progeny							F_2 Plant						
			Additive		Dominance					Additive		Dominance		
Chrom.	Pos. ‡	Locus	Effect §	Partial r^2 ¶	Effect	Partial r^2	Gene action #	Pos.	Locus	Effect	Partial r^2	Effect	Partial r^2	Gene action
						Ear length (genetic effects in cm)								
1	14	*UMC164*	0.3**	1.0	0.1	0.1	PD	26	*umc1071*	0.7**	3.4	–0.1	0.0	A
1	64	*NPI234*	0.5**	4.2	0.2	0.2	PD							
1	160	*NPI236*	–0.4**	3.2	0.3*	0.7	OD							
2	30	*UMC78*	0.2	0.5	0.4**	1.2	OD	44	*NPI287*	0.7**	3.7	0.9**	2.7	D
2								136	*UMC137*	0.7**	4.2	0.8**	2.3	D
3	22	*bnlg1523*	–0.3**	1.1	–0.1	0.0	PD							
3	102	*bnlg2241*	0.7**	7.7	0.0	0.0	A	114	*BNL10.24*	0.7**	4.0	0.3	0.3	PD
4	72	*umc1194*	–0.4**	2.1	0.2	0.4	D							
5								52	*ISU92*	0.4*	1.0	0.7*	1.3	OD
5	76	*bnlg105*	0.6**	4.5	0.3	0.6	D							
5								102	*ISU77*	–0.9**	5.8	1.1**	4.4	OD
5	128	*phi330507*	0.3**	1.2	0.3*	0.7	OD							

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

† QTL that share a row are considered the same based on overlapping 20-cM intervals.

‡ Position of highest LOD value in cM from the distal end of the short chromosome arm.

§ Positive and negative (–) values indicated an allele from LE-37 or SE-40, respectively, increased the trait's phenotype.

¶ Phenotypic variation (%) explained by the genetic effect after accounting for all other effects in the multiple-QTL model.

Level of dominance ($2d/a$ for $F_{2:3}$ and d/a for F_2) partitioned by published criterion (Stuber et al., 1987). A = additive (0–0.20); PD = partial-dominance (0.21–0.80); D = dominance (0.81–1.20); and OD = over-dominance (> 1.21).

†† Phenotypic variation explained by the multiple-QTL model adjusted for degrees of freedom.

Table 3. (cont.)

	$F_{2:3}$ Progeny							F_2 Plant						
			Additive		Dominance					Additive		Dominance		
Chrom.	Pos.	Locus	Effect	Partial r^2	Effect	Partial r^2	Gene action	Pos.	Locus	Effect	Partial r^2	Effect	Partial r^2	Gene action
6	0	*phi126*	0.5**	4.8	0.0	0.0	A							
6								32	*UMC59*	1.0**	6.4	0.0	0.0	A
6	100	*nc013*	0.7**	7.3	0.2	0.3	PD	112	*UMC160A*	1.3**	12.5	0.0	0.0	A
6	146	*bnlg1740*	0.6**	5.0	0.2	0.2	PD							
7	20	*NPI400*	0.3**	1.4	0.2	0.2	D							
7	66	*bnlg434*	0.4**	2.7	–0.2	0.2	PD							
9	48	*phi022*	–0.3	0.4	0.6**	1.7	OD	38	*NPI567*	0.9**	5.8	0.0	0.0	A
9	60	*umc1691*	0.7**	2.7	–0.3	0.4	PD							
σ_p^2 explained ††			---------- 70% ----------							---------- 54% ----------				
---------- Kernels per 5 cm (genetic effects in no. of kernels) ----------														
1								92	*bnlg1811*	0.7**	12.9	0.2	0.4	PD
1	128	*NPI429*	0.2**	2.4	–0.2**	1.5	OD							
1	214	*ISU6*	–0.3**	7.0	0.2*	1.5	D							
2	58	*UMC34*	–0.4**	9.3	0.1	0.1	PD							
2	152	*NPI210*	–0.2**	2.1	0.2*	1.0	OD							
3	46	*phi036*	0.2**	1.9	0.2	0.7	OD							
5								40	*bnlg1382*	–0.5**	6.1	–0.4**	2.7	D
5	100	*ISU77*	–0.2**	4.2	0.0	0.0	A							

Table 3. (cont.)

	$F_{2:3}$ Progeny							F_2 Plant						
			Additive		Dominance					Additive		Dominance		
Chrom.	Pos.	Locus	Effect	Partial r^2	Effect	Partial r^2	Gene action	Pos.	Locus	Effect	Partial r^2	Effect	Partial r^2	Gene action
6	28	*bnlg1371*	–0.2**	2.0	0.0	0.0	A							
7	94	*BNL14.07*	–0.1	0.4	0.3**	2.4	OD							
8	2	*bnlg1194*	0.2**	2.6	0.0	0.0	PD							
8	44	*phi115*	–0.3**	5.9	0.1	0.4	PD							
9	50	*phi022*	–0.3**	5.0	0.2*	1.1	OD	40	*NPI567*	–0.4**	4.0	–0.1	0.2	PD
10	24	*umc1077*	0.2**	2.5	0.2*	1.2	OD							
σ_p^2 explained			---------- 62% ----------							---------- 26% ----------				

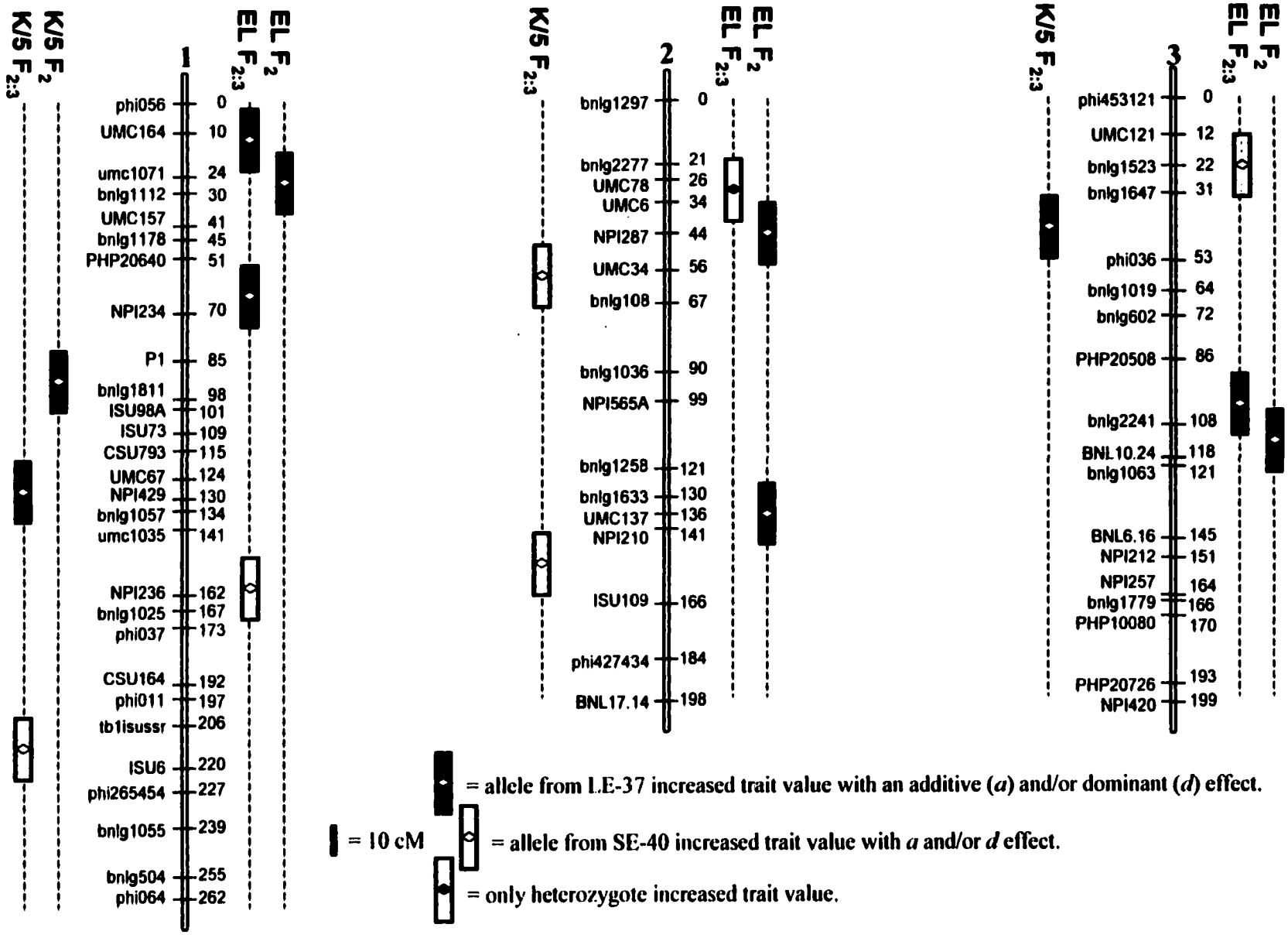

Figure 1. QTL for EL and K/5CM identified among 188 $F_{2:3}$ progeny and their parental F_2 plants from the SE-40×LE-37 maize population.

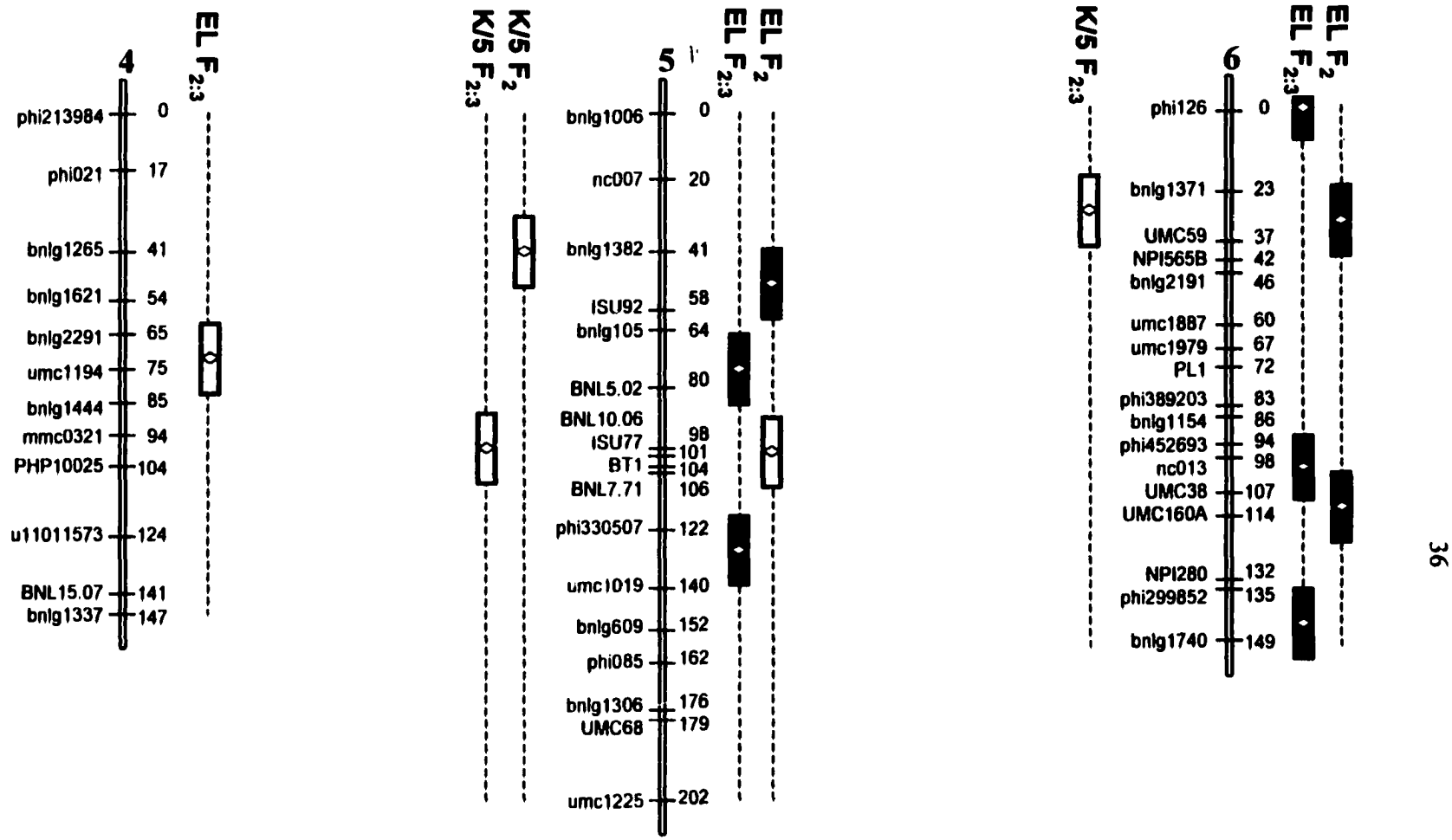

Figure 1. (cont.)

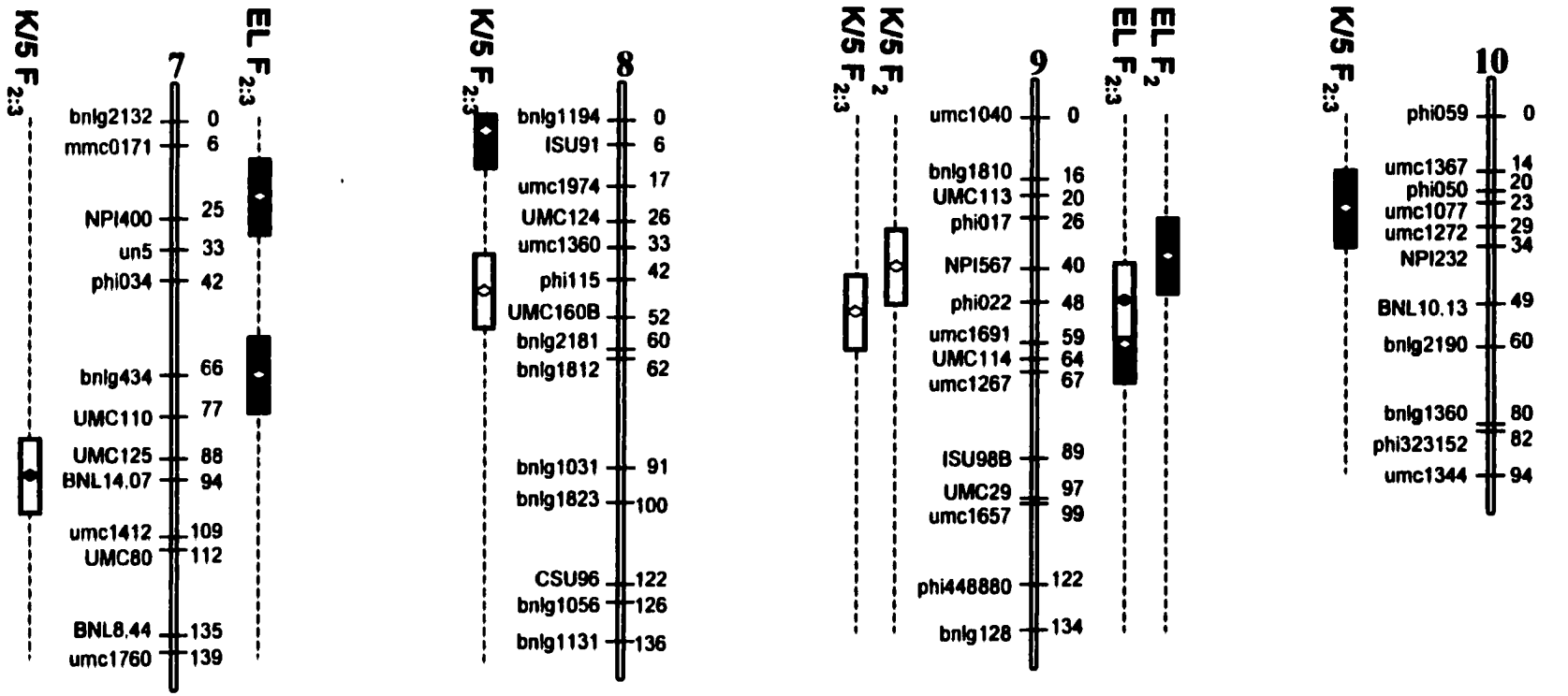

Figure 1. (cont.)

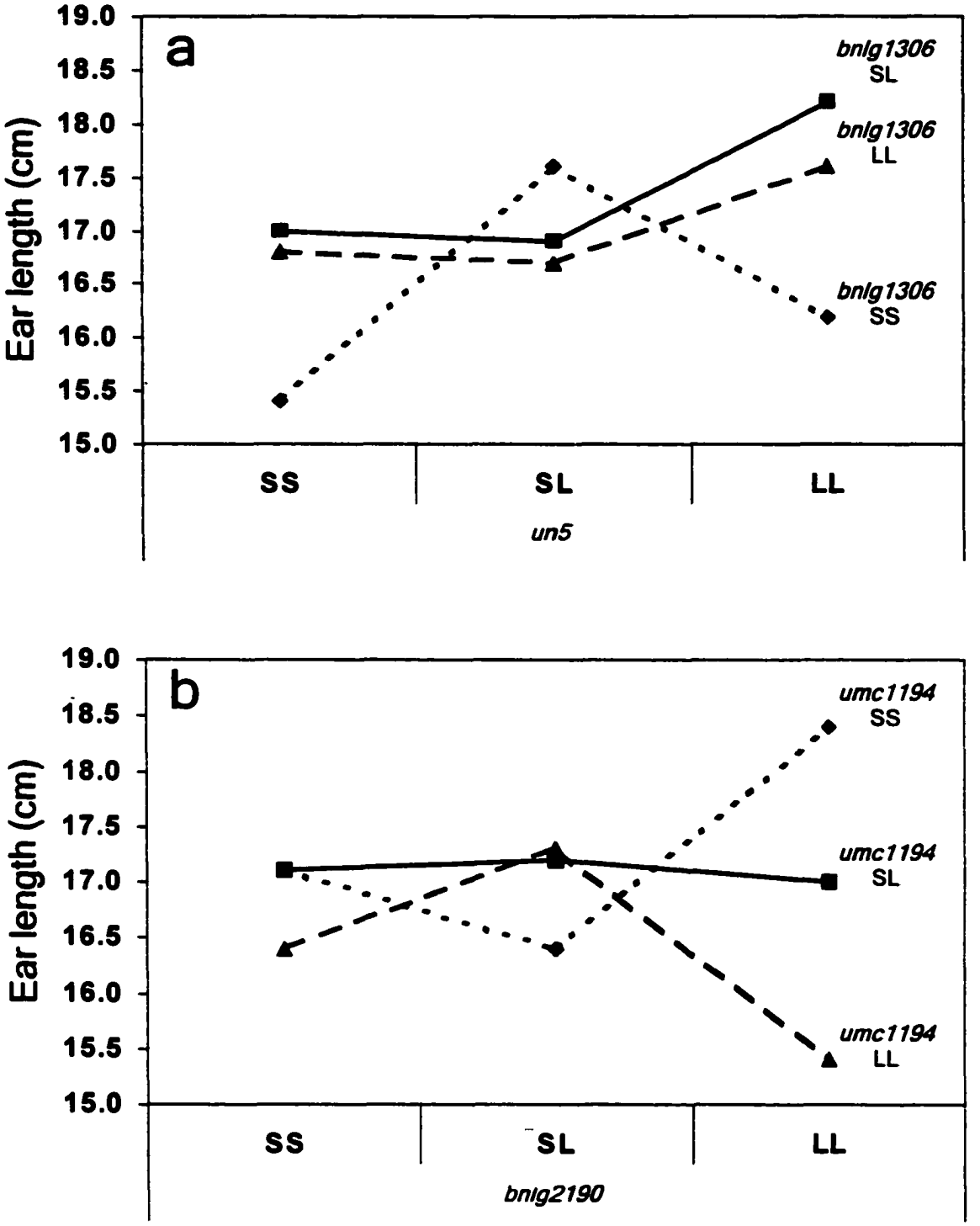

Figure 2a–b. Interaction plots for ear length means of $F_{2:3}$ progeny from the SE-40×LE-37 maize population evaluated in 2001. S is an allele from SE-40 and L is an allele from LE-37. **a** Interaction effect of genetic regions marked by *un5* and *bnlg1306* (*d* × *a*). **b** Interaction effect of genetic regions marked by *bnlg2190* and *umc1194* (*d* × *a*).

CHAPTER 3.
GENETIC ANALYSIS OF TRAITS CORRELATED WITH MAIZE EAR LENGTH

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Abstract

Ear length is a component of maize (*Zea mays* L.) grain yield. Thirty generations of selection for increased ear length, however, failed to increase grain yield in the Iowa Long-Ear Synthetic (BSLE). Negative correlations between ear length and other yield-related traits complicated selection for grain yield. This investigation was conducted to map and validate quantitative trait loci (QTL) for grain yield and traits correlated with ear length and to determine genetic regions causing trait correlations. A population developed from inbreds divergent for ear length (derived from the long-ear and short-ear generation 24 sub-populations of BSLE), and previously used to map ear length QTL, was used for this investigation. Genotypes and phenotypes of 188 F_2 plants and their $F_{2:3}$ progeny replicated twice in four environments were used for QTL analyses. More QTL were mapped for kernel-row number (10 in the F_2; 12 in the $F_{2:3}$) and kernel depth (7; 6) than in prior studies. QTL in the $F_{2:3}$ explained more than 50% of the kernel-row number and kernel depth variation, and most alleles had additive effects. Only three QTL in each generation were mapped for grain yield. Collectively, 52% of the kernel-row number, kernel depth, and grain yield QTL mapped in the $F_{2:3}$ were previously identified in the F_2. The number of coincidental QTL followed the trends of heritability. Genetic regions affecting trait correlations were identified. The cluster of QTL on chromosome 5 exemplified the genetic basis for the failure of ear length selection to increase grain yield in BSLE because of repulsion-phase linkage between QTL of the two traits. QTL on chromosome 6 may partially explain the positive correlation between ear length and grain yield.

Introduction

Maize ear length has received extensive research attention because it inherently limits the amount of grain a single inflorescence may bear. The positive correlation of ear length with grain yield is evident in many genetic backgrounds and the average genetic correlation coefficient between

the two traits is 0.38 (Hallauer and Miranda, 1988). Because variation for ear length was associated with grain yield (Robinson et al., 1951), maize breeders hypothesized this positive relationship could be used to indirectly select for increased grain yield by selecting on the more heritable and easily measured trait, ear length. To determine if indirect selection would enhance the genetic gain for grain yield, maize breeders at Iowa State University conducted divergent mass selection on ear length in the Iowa Long-Ear Synthetic (BSLE). BSLE was formed from 12 long-eared inbreds (Russell et al., 1971) that represented germplasm from varying populations and heterotic groups within the Corn Belt Dents (Hallauer et al., 2003; Ross et al., 200X).

Results from a Design I experiment conducted in BSLE indicated that the correlation between ear length and grain yield was not as large as reported in other open-pollinated populations (Hallauer, 1968). The genetic correlation coefficient (r_g) between ear length and grain yield was 0.38, but the additive genetic correlation coefficient (r_a) was only 0.03. In addition, the coefficient of simple determination indicated the phenotypic variation in grain yield attributable to ear-length variation was only 20%.

Divergent selection was conducted in the BSLE long-ear [BSLE(M-L)] and short-ear [BSLE(M-S)] sub-populations for 30 cycles. The direct response to selection for ear length and correlated responses of other traits were monitored at cycles 10 (Cortez-Mendoza and Hallauer, 1979), 15 (Salazar and Hallauer, 1986), and 27 (Lopez-Reynoso and Hallauer, 1998). A comprehensive review of the BSLE selection experiment was provided by Hallauer et al. (2003). Results from BSLE investigations displayed the effectiveness of mass selection to alter ear length and cause correlated changes in other ear and plant traits. The mean ear-length difference between the cycle 27 sub-populations of BSLE was > 14 cm and resulted from a linear increase of 0.27 ± 0.03 cm cycle^{-1} in BSLE(M-L) and a decrease of -0.37 ± 0.03 cm cycle^{-1} in BSLE(M-S). Grain yield remained unchanged in BSLE(M-L), but was significantly reduced in BSLE(M-S). The lack of an indirect response for grain yield with the selection of longer ears was attributed to the significant reduction in kernel-row number, ear diameter, and kernel depth, which are positively correlated with grain yield, but negatively correlated with ear length (Hallauer and Miranda, 1988). These traits were significantly increased in BSLE(M-S), but the $\approx$ 10 cm decrease in ear length resulted in the significant reduction of grain yield.

The change in trait values in the BSLE divergent sub-populations indicated the relationship of grain yield and other ear traits with ear length was founded on a genetic basis. These relationships were not attributed to genetic drift because the effective population size was estimated to be $\approx$ 4 000 individuals for each sub-population (Hallauer et al., 2003).

To investigate the inheritance and correlations among ear length, grain yield, and other ear traits at the genetic level, inbreds derived from the BSLE cycle 24 sub-populations were used to develop a F_2 population to map QTL. The identification and characterization of 16 QTL affecting ear length variation in this population was reported by Ross et al. (200X). The investigation presented herein, mapped QTL affecting grain yield and other ear traits in the F_2 and $F_{2:3}$ generations of the same population and environments used to study ear length. Data on ear length were also provided to facilitate the comparison of the number and position of QTL contributing to the phenotypic variation of each trait.

The objectives of this investigation were to 1) determine the genetic positions and effects of QTL for grain yield and ear traits correlated with ear length, 2) validate QTL by comparing QTL positions obtained in the F_2 and $F_{2:3}$ generations, and 3) determine if QTL positions explain trait correlations and correlated responses to selection for ear length in the BSLE sub-populations.

Materials and Methods

Plant Materials

Ross et al. (200X) described the development of S_6 inbreds from the cycle (C) 24 sub-populations of BSLE. SE-40 was determined to have the shortest ear length from inbreds originating from BSLE(M-S) C24 and LE-37 the longest ear length from inbreds originating from BSLE(M-L) C24. A bi-parental F_2 population was developed from a single F_1 plant from the cross SE-40 × LE-37. Ross et al. (200X) provided detailed descriptions of the development of random $F_{2:3}$ progeny, genotypic evaluation, and the genetic map of SE-40×LE-37. Brief descriptions of methods and procedures related to those events were provided herein.

Phenotype Evaluation

Phenotypic data for this experiment were collected on individual F_2 plants in 2000 and their corresponding $F_{2:3}$ progeny in 2001. At the Agronomy and Agricultural Engineering Research Center near Ames, IA on 10 May 2000, 510 F_2 kernels from SE-40×LE-37 were hand-planted at a seeding rate of 2 kernels $hill^{-1}$ in rows 5.5 m in length. Adjacent rows were spaced 0.76 m and 0.30 m separated hills within a row. Hills were thinned to one F_2 plant at the V4 growth stage (Ritchie et al., 1996). Four rows for each parent and their F_1 were planted at 5 d intervals (–5, 0, and +5) relative to planting the F_2 kernels and were maintained with the F_2 rows. The parent and F_1 plants served as a homogenous genetic source for estimating environmental variation.

Each F_2 plant was self-pollinated for three consecutive days after male anthesis was 50% complete. This pollination method was implemented to avoid biasing trait phenotypes due to

unpollinated spikelets on the terminal end of the rachis. At maturity, all ears on each competitive F_2 plant were hand-harvested, dried, and data for five ear traits were obtained from each plant. Ear length (EL), kernel-row number (KRN), kernel depth (KD), and kernel weight (KWT) were evaluated on the primary ear. EL was measured from the base to the terminal end of the rachis and recorded in centimeters. KRN was the number kernel rows at the middle of the ear. KD, expressed in centimeters, was calculated by subtracting the cob diameter from the ear diameter and dividing the difference by two. KWT was the weight in grams of a 300-kernel sample. Grain yield (GY) was evaluated on a plant basis by weighing all kernels produced and recorded in grams plant^{-1}. Data from 120 open-pollinated plants (40 from each planting interval) of each parent and their F_1 were also collected.

A random sample of 189 F_2 plants was taken from the population and evaluated in replicated-progeny rows in 2001. The 189 $F_{2:3}$ progeny and 11 other entries [three entries each of LE-37, SE-40, and SE-40×LE-37, and one entry each of (SE-40×LE-37)×SE-40 and (SE-40×LE-37)×LE-37] were randomized to single-row plots of a 10×20 row-column lattice experiment. The experiment was evaluated in two replications near Ames, Ankeny, Crawfordsville, and Lewis, IA. Plots were 5.5 m in length and 0.76 m separated adjacent plots. Plots were machine planted at Ames on 26 April, Crawfordsville on 02 May, and Lewis on 27 April 2001 at a seeding rate of 30 kernels plot^{-1} (71 700 kernels ha^{-1}) and hand-planted at Ankeny on 15 May 2001 at a rate of 2 kernels hill^{-1} with 15 hills plot^{-1}. Plots were thinned at V5–V7 to 15 plants plot^{-1} (35 900 plants ha^{-1}). This plant density was used for evaluation of F_2 plants in 2000, and was maintained across F_2 and $F_{2:3}$ generations to minimize environmental variation. At maturity, the primary ear from the first 10 competitive plants per plot was hand-harvested and dried at 38 C for 4 d. Plot means were obtained for EL, KRN, and KD from the 10 primary ears. The plot mean for GY was obtained from the total weight of all kernels produced on 10 plants, and KWT was determined from a 300-kernel sample of the total shelled grain.

Phenotype Analysis

Phenotype data were analyzed from the F_2 and $F_{2:3}$ generations. One F_2 plant and its progeny were excluded from all analyses because data on cob color (*P1* locus) were not consistent across generations, indicating that the F_2 plant was not self-pollinated. For data analysis in the F_2 generation, the mean and variance were computed for each trait within each source of plants (SE-40, LE-37, F_1, and F_2) grown in 2000. The variances were used to calculate broad-sense heritabilities (h^2) on a plant basis as described by Weber and Moorthy (1952).

Plot means of each trait were used for data analysis in the $F_{2:3}$ generation. The plot means at each environment were adjusted for intrablock effects from a lattice analysis that included rows and

columns as random sources of variation. The adjusted least-square means from each environment were used in the analysis of data combined across environments (mean environment). The combined analysis was performed using a general-linear model with environments, entries, and their interaction considered random sources of variation. For each trait, the sums of squares for entries and entries × environment were partitioned into among $F_{2:3}$ progeny, among checks, and the orthogonal contrast. *F*-tests were used to determine the significance of each source of variation.

Only sources of variation due to the $F_{2:3}$ progeny and the $F_{2:3}$ progeny×environment interaction were used in calculating h^2, variance components, and phenotypic and genotypic correlation coefficients. Heritability on a progeny-mean basis and the 95%-confidence interval of h^2 were computed according to Knapp et al. (1985). Heritability also was estimated by regressing $F_{2:3}$–progeny means onto F_2 plant values. Phenotypic correlation coefficients were computed in the F_2 and $F_{2:3}$. Genotypic correlation coefficients, and their approximate standard errors, were computed according to Mode and Robinson (1959).

Genetic Map

DNA collection, genotype evaluation, and genetic map construction were previously described by Ross et al. (200X). Briefly, DNA was obtained from the 188 F_2 plants and genotyped at 160 co-dominant marker loci. The majority of the markers were SSR (97), hereafter in lowercase text, and RFLP loci (62), hereafter in uppercase text. The genetic map represented the 10 maize chromosomes and had a cumulative distance of 1662 Haldane centimorgans (cM) with a median distance between loci of 10 cM.

Genetic Analysis

Identification of QTL affecting EL variation was completed by Ross et al. (200X). QTL detection for KRN, KD, GY, and KWT were completed using the same procedures and significance thresholds used for QTL analysis of EL. QTL were detected using the regression-based method of composite interval mapping (CIM; Zeng, 1994) employed by the computer program PLABQTL version 1.1 (Utz and Melchinger, 1996). The analysis was completed using a series of PLABQTL runs. The initial run was completed with the "cov sel" command that selected cofactors (marker loci) using stepwise regression with the program's default *F*-to-enter (to-drop) threshold of 3.5. The second run was done by setting all marker loci as cofactors ("cov/+sel" command) that may allow linked QTL with opposite effects to be resolved. The marker loci closest to each detected QTL in the initial or second runs were used as cofactors in a third run. If new QTL were detected in this run, they were fitted in a following run. This procedure was continued until no new QTL were detected. As suggested by Holland et al. (2002), if different QTL were detected in the series of runs, subsets of

these QTL were tested. A model stipulated by cofactors being linked to QTL (Zeng, 1994) with significant ($P < 0.05$) genetic effects and having the lowest Akaike's information criterion (Jansen, 1993) was chosen as the final multiple-QTL model. To determine the amount of phenotypic variation that a defined group of QTL may explain, the "seq" statement was used. QTL of interest were deleted from the final multiple-QTL model and the remaining QTL were used as regressors. The difference between the coefficient of multiple determination (R^2) between the full and reduced-models was considered the amount of phenotypic variation that the deleted-QTL group explained.

To be consistent with the definition of EL QTL (Ross et al., 200X), the presence of a QTL was declared at the likelihood of odds (LOD) threshold of 2.5 and defined as 20-cM interval. Defining QTL as a constant genetic-map interval has been completed in other experiments (Melchinger et al., 1998; Cardinal et al., 2001; Holland et al., 2002) because one-LOD support intervals are often underestimated and determining confidence intervals for QTL from CIM remains unresolved (Visscher et al., 1996). The additive effect (a) and dominance deviation (d) were calculated for each QTL (Falconer and Mackay, 1996). Gene action was assigned to each QTL based on the level of dominance and the criteria defined by Stuber et al. (1987): additive (A) = 0–0.20; partial-dominance (PD) = 0.21–0.80; dominance (D) = 0.81–1.20; and over-dominance (OD) > 1.21. The level of dominance for F_2 plants was defined as d/a and for $F_{2:3}$ progeny as $2d/a$. The ratios differ between generations because at a given locus only half of the $F_{2:3}$ plants would exhibit dominance; therefore, the dominance effect was doubled for determining gene action. The phenotypic variation explained by the genetic effects (a or d) at each QTL was estimated with a partial r^2 value computed by dividing the partial sums of squares for each effect by the total sums of squares for the regression model (Holland et al., 1997, 2002). Partial r^2 values computed in this manner will not sum to more than the adjusted-R^2 for the multiple-QTL model, unlike partial r^2 values computed by PLABQTL (Holland et al., 2002).

Digenic epistasis was estimated between all possible pairs of marker loci using EPISTACY (Holland, 1998). A comparison-wise threshold of $P < 0.00026$ was used to declare interactions significant. This threshold was a liberal Bonferroni-style significance level computed by assuming each of the 20 chromosome arms was an independent group ($n = 190$). Marker loci involved in an interaction were added to a multiple-regression model with marker loci nearest each QTL detected by PLABQTL. Interaction terms that remained significant ($P < 0.05$) in the regression model and increased the adjusted-R^2 of the model were considered important for a trait's heredity.

QTL analysis was completed on five sets of phenotypic data for each trait: F_2–plant values, adjusted-$F_{2:3}$–progeny means from each of four environments, and entry means from the $F_{2:3}$ mean

environment. To determine if QTL were identified in different analyses, the map positions of QTL were compared. If QTL (20-cM interval) overlapped then the QTL were considered identical. To compare the location of QTL to those found in other populations, a 20-cM interval redefined the boundaries of QTL in other populations and comparisons were aided with the linkage to common marker loci.

Results

Phenotype Analysis

The means, ranges, and h^2s for each trait evaluated on a plant (2000) and entry-mean basis (2001) are presented in Table 1. Data on GY, KWT, and KD were either not available or obtained from a small number of plants or plots for SE-40 and/or LE-37. The flowering characteristics of the parents hindered fertilization and kernel development, which affected the measurements of GY, KWT, and KD. SE-40 and LE-37 were in the later 2% of the genotypes to reach female anthesis, and had above-average delay of female anthesis compared with male anthesis (unpublished data, Ames, IA, 2001). Comparison of F_2 and $F_{2:3}$ trait means was facilitated by their relation to F_1 means. All trait means in the $F_{2:3}$ (2001) had a greater divergence from the F_1 means than existed between F_2 and F_1 means in 2000. The difference between progeny and F_1 means increased more for KRN (50%) and less for KWT (22%) and may be attributed to environmental effects and/or level of inbreeding of each generation. The ranges of the $F_{2:3}$ phenotypes were reduced compared with ranges in the F_2 for EL (46%), GY (17%), KWT (34%), and KRN (43%), but not for KD. This reduction probably occurred because of the more precise estimates of $F_{2:3}$ phenotypes as previously suggested by Ross et al. (200X).

Heritability on a progeny-mean basis was high (0.94 to 0.76) for all traits (Table 1). Lamkey and Hallauer (1987) reported that h^2s estimated from S_1 or S_2 progenies are often of this magnitude. High progeny-mean h^2s were expected because the differences among $F_{2:3}$–progeny means were highly significant and there were no $F_{2:3}$–progeny×environment interactions for any trait except KWT. EL and KRN were the most heritable (0.94) traits and KWT the least (0.76). This trend was generally observed for h^2s estimated on a plant basis and by F_2–$F_{2:3}$ (parent-offspring) regression (Table 1).

Correlation coefficients among the five traits within each generation are presented in Table 2. The direction of all phenotypic correlation coefficients (r_ps) was consistent between generations, but the magnitude and significance of the r_ps were generation dependent. The genotypic correlation coefficients (r_gs), were similar in magnitude to their corresponding r_ps, indicating that the correlations

were not due to environmental effects. EL had positive r_ps with GY and KWT and negative r_ps with KRN and KD in each generation. Genotypic correlation coefficients in the $F_{2:3}$ were significant and of similar magnitude for EL with GY (0.22), KRN (–0.28), and KD (–0.29). Positive and significant r_ps and r_gs existed between GY and every trait, except KWT in the $F_{2:3}$. The three largest r_gs were between GY and KD (0.73), GY and KRN (0.44), and KRN and KD (0.61).

Correlations between KWT and other traits were less than expected. KWT was not associated with EL, GY, or KD in the $F_{2:3}$ and the agreement of r_ps involving KWT was lacking between generations. Because of these poor and inconsistent associations with the other traits, and KWT's below-average h^2, KWT was excluded from further analyses and discussions presented herein. (The genetic positions and effects of KWT QTL in the F_2 and $F_{2:3}$ are presented in the Chapter 3 Appendix – Table 1 and Figure 1).

Genetic Analysis

A total of 29 QTL in the F_2 and 74 in the $F_{2:3}$ were detected for the four traits (Table 3). EL and KRN, which had the highest h^2 (0.94), had the most QTL identified (9 and 26 for EL; 10 and 23 for KRN). GY had the least number of QTL (3 and 6) identified in each generation. For each trait in the $F_{2:3}$, except KD, ≥ 50% of the total QTL were detected in the mean environment. QTL not detected in the mean environment were mostly (> 70%) observed in one $F_{2:3}$ environment. Additionally, a greater percentage of QTL for EL (27%), GY (17%), and KRN (17%) were identified in the mean environment than the average number of QTL identified across environments. Because of the preceding observations, the mean environment was the focus of further discussions regarding the $F_{2:3}$ generation.

Five more QTL for EL and two more for KRN were detected in the mean environment of the $F_{2:3}$ compared with the number of QTL detected in the F_2. No increase was observed for the number of GY QTL, and a decrease of one QTL occurred for KD between the $F_{2:3}$ and F_2 analyses. Replicated progeny did not seem to increase the number of QTL detected. Although, it may be that more of the QTL from the F_2, than the $F_{2:3}$, were false-positive detections (type I errors); as the quality of F_2 phenotype data was limited by measurements of individual plants. Similar reasoning limited the confidence of QTL identified at any one $F_{2:3}$ environment.

Validation of QTL was attempted by identification of the QTL in different environments and/or generations. Most QTL identified in the $F_{2:3}$ mean environment were detected in two or more individual environments. For example, 83% (10/12) of the KRN QTL in the mean environment were detected in at least two individual environments (Table 3). Averaged across traits, 73% (27/37) of the QTL in the $F_{2:3}$ mean environment were detected at two or more environments. EL, with the most,

had four QTL detected in the mean environment and all four individual environments. Forty-three percent (16/37) of the QTL from the F_2 were validated by detecting the same QTL in the $F_{2:3}$. EL, KRN, and KD each had more than four QTL from the F_2 validated, but only one QTL was consistent between generations for GY. Only a QTL for EL on chromosome 6 and a QTL for GY on chromosome 5 were detected in all six generation-environment combinations.

The presentation and discussion of QTL identified for EL (9 in the F_2 and 16 in the $F_{2:3}$) were previously reported by Ross et al. (200X) and results will not be repeated herein. The location and genetic effects of QTL for GY, KRN, and KD, detected within each generation, are presented in Table 4. Three GY QTL were identified in each generation and explained ≈ 35% of the phenotypic variation. QTL in the F_2 were on chromosomes 2, 3, and 5, and in the $F_{2:3}$ on 5, 6, and 10. The QTL on chromosome 5 was detected in both generations and had the largest effects ($a > 12$ and $d > 8$ g plant^{-1}) on GY. An allele from SE-40 increased GY at this QTL in each generation, and the QTL explained 24% of the phenotypic variation among F_2 plants and 31% among $F_{2:3}$–progeny means. LE-37 provided the allele that increased GY at the QTL on chromosome 6 in the $F_{2:3}$. The parental origin of the other GY alleles could not be determined because additive effects at those QTL were not significant. Dominance effects of QTL were more prevalent than additive effects in both generations and gene action was classified as over-dominance for 2 of 3 QTL in the F_2 and all three QTL in the $F_{2:3}$.

Contrary to GY, KRN had a large number of QTL identified in the F_2 (10) and $F_{2:3}$ (12), and QTL were dispersed throughout the genome. QTL in the F_2 explained 47% of the KRN variation, and in the $F_{2:3}$ 63% was explained. Additive effects were significant at all QTL, and only two QTL, in each generation, had significant dominance effects. Seventy percent of QTL in the F_2 and 83% in the $F_{2:3}$ had an allele from SE-40 that increased KRN. QTL with the largest effects on KRN were identified on chromosome 1 in each generation (1.2 kernel rows in the F_2 and 0.7 rows in the $F_{2:3}$).

The difference between parental genotypes ($2a$), averaged across QTL, was 1.5 kernel rows in the F_2, and 0.7 in the $F_{2:3}$. The average effect in the F_2 was twice the effect of the $F_{2:3}$. Ross et al. (200X) observed a similar trend for EL, and provided possible explanations for difference of effects between generations. Gene action was primarily additive and partial-dominance at KRN QTL in the F_2, and partial-dominance and dominance in the $F_{2:3}$. Six KRN QTL coincided between generations, but the largest two QTL in the $F_{2:3}$ were not detected in the F_2. These six QTL were each identified in two or more individual $F_{2:3}$ environments (data not shown).

Unlike other traits, KD had more QTL identified in the F_2 (7) than in the $F_{2:3}$ (6). QTL in the $F_{2:3}$ explained 46% of the KD variation, but QTL in the F_2 only explained 29%. This difference was

probably due to a single QTL on chromosome 5 (*BNL10.06*). The genetic effects at this locus explained 20% of the KD variation among $F_{2:3}$–progeny means but only 5% among F_2 plants. The increase in KD, at all but one QTL, was provided by alleles from SE-40. Additive effects were significant at all but one QTL, and dominance effects were important at ≈ 70% of the QTL in the $F_{2:3}$, but only ≈ 30% in the F_2. The average additive effect of an allele was consistent across generations and was 0.03 cm. KD had four QTL that coincided between generations. As a ratio of coinciding QTL to QTL detected in the $F_{2:3}$, KD (4/6) had a higher coincidence of QTL than other traits.

Epistatic interactions accounted for additional amounts of phenotypic variation, when added to the main-effect multiple-QTL model (from Table 4), for GY and KRN in each generation and KD in the F_2. A summary of the interactions is presented in Table 5. Sixty-seven percent of the marker loci contributing to epistatic interactions had no significant main effect, and most were > 20 cM from any main-effect QTL (see Figure 1) detected for the same trait and generation.

Digenic epistasis for GY was identified between a pair of loci in the F_2 and three pairs in the $F_{2:3}$. An increase of 5 percentage points of GY variation explained in the F_2 was attributed to a single interaction. Three interactions in the $F_{2:3}$ cumulatively increased the phenotypic variation explained for GY by 14 percentage points. KRN and KD in the F_2, also had significant increases in variation explained when all significant interactions were considered (Table 4).

All interactions occurred between genes on different chromosomes except for the interaction of *umc1691* and *umc1657*; which both map to (40 cM apart) chromosome 9. No main-effect QTL was identified for KRN in the F_2 on chromosome 9. However, two QTL, one near each of the marker loci contributing to the interaction in the F_2, were identified in the $F_{2:3}$ (Figure 1). An interaction between these KRN QTL was also observed in the $F_{2:3}$ but the failed to meet the significance threshold.

Discussion

This investigation identified 10 and 12 QTL for KRN and 7 and 6 QTL for KD in the F_2 and $F_{2:3}$ generations, respectively. Other studies with comparable population sizes (100–200 individuals) and QTL identification techniques have not identified as many QTL (Beavis et al., 1994; Veldboom and Lee, 1994, 1996; Austin and Lee, 1996). The three GY QTL identified in each generation was within the range of GY QTL observed in other populations.

The increased number of QTL identified within the generations of SE-40×LE-37 compared with other populations may have resulted from several causes. First, the genetic background of populations was different and a unique subset of alleles was probably segregating in each population.

Second, SE-40 and LE-37 were the result of ≈ 30 generations of divergent selection for EL, and the correlated response of KD and KRN with EL were also divergent; with shorter ears having increased KRN and KD (Lopez-Reynoso and Hallauer, 1998; Salazar and Hallauer, 1986). The divergence of alleles that increased KRN and KD should have increased the probability of these alleles being in association for each trait, which benefits the detection of QTL (Falconer and Mackay, 1996); QTL were in association for these traits in SE-40×LE-37, with 80% of the alleles that increased KRN, and 90% for KD, originating from SE-40. Third, the amount of replication in the $F_{2:3}$ of SE-40×LE-37 was greater than replication of previous studies and the population size was larger, albeit by < 2% for Austin and Lee (1996), and < 40% for Beavis et al. (1994). Fourth, environmental signals in different years of phenotype evaluation may have affected QTL detection.

QTL Validation

Validation of QTL from SE-40×LE-37 provided additional confidence that QTL were not false-positive detections. Several methods and combinations of methods for validating QTL have been completed in QTL studies. The methods were 1) comparison of QTL across environments (e.g., Stuber et al., 1992; Austin and Lee, 1998), 2) across samples (e.g., Beavis, 1994; Melchinger et al., 1998), 3) across non-successive generations (e.g., Austin and Lee, 1996, 1998); across populations (e.g., Stuber et al., 1987; Abler et al., 1991), 4) across testers for hybrid progeny (e.g., Melchinger et al., 1998; Austin et al., 2000), 5) by fine mapping QTL (e.g., Graham et al., 1997), and 6) by cloning QTL (e.g., Doebley et al., 1997; Frary et al., 2000). These methods, however, prolong research and increase expenditures for additional progeny development, and genotype and phenotype evaluation. Comparing QTL detected from individual plants and their derived progeny (F_n and $F_{n:n-}$) requires only a slight increase in research costs. The genetic information applies to both generations, and phenotype evaluation is completed in the same growing seasons as progeny development. Surprisingly, this validation method has not received much use in maize investigations, with the exception of Holland et al. (1998). Validation by this successive-generation method should complement other validation methods as it has provided further assurance of QTL positions and effects in the F_2 and $F_{2:3}$ of SE-40×LE-37.

Validation and the coincidence of EL QTL across generations of SE-40×LE-37 were discussed by Ross et al. (200X). Collectively, 52% of the QTL for GY, KRN, and KD detected in the $F_{2:3}$ were previously identified in the F_2 generation. KRN had the most QTL (6) coinciding between generations. In addition, epistasis analyses for KRN indicated that an interaction between two QTL (near *umc1691* and *umc1657* on chromosome 9) in the F_2 explained additional phenotypic variation. These QTL were not identified as main-effect QTL in the F_2, but were identified in the $F_{2:3}$.

Considering these QTL to be coincidental, indicated that 67% of the KRN QTL in the $F_{2:3}$ were identified from individual plant data. In general, the number of coincidental QTL between generations followed the trend of progeny-mean h^2s. QTL not coinciding between generations were not necessarily false-positive detections, but may have variable effects under different environmental signals. For example, a GY QTL on chromosome 3 detected in the F_2 was not detected in the $F_{2:3}$–mean environment, but was detected, with the same genetic effect, at the Ames $F_{2:3}$ environment. The surprising result of validation by comparing QTL in the F_2 and $F_{2:3}$ was 16 verified QTL identified from individual-plant data.

QTL Detected in Other Populations

The consistency of QTL positions across populations provides further assurance that QTL were not false-positive detections. Also, QTL detection in several populations may indicate which QTL are not dependent on the genetic background. Ross et al. (200X) reported that 7 of 16 QTL identified in SE-40×LE-37 coincided with QTL in the $F_{2:3}$ and/or $F_{6:7}$ generations of Mo17×H99 (Austin and Lee, 1998). QTL for GY and KRN identified SE-40×LE-37 also coincided with QTL detected in other populations and progeny types. A KRN QTL on chromosome 4 (near *umc0321*, see Figure 1) was identified in both generations of SE-40×LE-37, the $F_{2:3}$ and $F_{6:7}$ of Mo17×H99 (Austin and Lee, 1996), and the $F_{2:4}$ of B73×Mo17 (Beavis et al., 1994). The increase in KRN was associated with an allele from LE-37, Mo17 (Austin and Lee, 1996), and B73 (Beavis et al., 1994). The positive effect originating from both B73 and Mo17 may indicate that multiple alleles segregate at this locus or the QTL represents the effect of more than one gene.

The largest GY QTL was identified on chromosome 5 (*ISU77*) in each generation of SE-40×LE-37. From progenies of B73×Mo17, Stuber et al. (1992) also found a major QTL at this region. Further characterization partitioned the QTL identified by Stuber et al. (1992) into two QTL linked in repulsion (Graham et al., 1997). Of these two QTL, the locus with the largest effect corresponded to the QTL detected at *ISU77* in SE-40×LE-37. Visual observation of likelihood plots from PLABQTL, using all markers as cofactors, indicated two GY QTL, linked in repulsion, may be at this region in SE-40×LE-37 (see Chapter 3 Appendix – Figure 2). The genetic resolution of SE-40×LE-37, however, would not permit the separation of these QTL. The GY QTL identified on chromosome 6 of SE-40×LE-37 was detected in every environment-generation ($F_{2:3}$ and $F_{6:7}$) combination of a Mo17×H99 population (Veldboom and Lee, 1996; Austin and Lee, 1998). This QTL, however, was not identified in either generation of Mo17×H99 when progenies were evaluated in hybrid combinations (Austin et al., 2000).

Trait Correlations and Relation of QTL Positions

The correlation coefficients obtained from SE-40×LE-37 had the same direction as coefficients from BSLE C0 (Hallauer, 1968), and average coefficients from populations summarized by Hallauer and Miranda (1988). QTL positions and the parental origin of alleles that increased trait values agreed with the direction of r_gs in SE-40×LE-37 (Figure 1), and were in accordance with the inability to indirectly increase GY by selection on EL in the BSLE experiment (Hallauer et al., 2003).

EL had the lowest r_g (0.22) with GY compared with the r_gs of GY with KRN (0.44) and KD (0.73). The magnitude of r_gs was generally explained by the frequency of QTL located at the same genetic position or in linkage disequilibrium. QTL for EL in the $F_{2:3}$ did not coincided at the same genetic position, but were linked in coupling and repulsion, to GY QTL. Contrarily, KRN and KD QTL often shared genetic positions with GY QTL and alleles from the same parent. The primary examples were on chromosomes 2 (*bnlg1297–bnlg2277*), 3 (*NPI257*), and 5 (*ISU77*). Determining the genetic basis of correlations with GY was limited because few GY QTL were mapped compared with ear trait QTL.

The resolution of the SE-40×LE-37 genetic map did not determine the definite causes (pleiotropy and linkage) of genetic correlations. But limited evidence for the causation of trait correlation was obtained from QTL positions. The r_g for KRN with KD was 0.61, and three QTL (chromosomes 1, 3, and 5) with alleles from SE-40 coincided for these traits, indicating that pleiotropy may cause their r_g. The largest r_g (0.73) was between GY and KD, and a QTL for KD coincided or was linked to each GY QTL, except for the loci on chromosomes 6 and 10. EL was negatively correlated ($r_g \approx -0.30$) with KRN and KD. In the $F_{2:3}$, QTL for EL and KRN coincided on chromosomes 1 and 9, and were linked in repulsion on four chromosomes. Only a QTL in the F_2 on chromosome 5 affected both EL and KD. Linkage of EL and KD QTL was less frequent than between EL and KRN. The negative correlation between EL and KD may be partially due to the correlation of both traits with KRN.

QTL positions provided information regarding the failure to increase GY and the correlated responses of KRN and KD, from selection on EL in the BSLE sub-populations. The cluster of QTL (*bnlg105–umc1019*) on chromosome 5 is a good example. Two EL QTL in the $F_{2:3}$ flanked the largest GY and KD QTL, and the second largest KRN QTL. These QTL were linked in repulsion, with the alleles increasing EL originating from LE-37 and the allele increasing GY, KRN, and KD from SE-40. Understanding the affect of ear traits on GY variation at this region was further complicated by the presence of a QTL in the F_2 that increased EL by a SE-40 allele (Figure 1). Selection on EL at this region would decrease the probability of simultaneously increasing GY. An

additional hindrance to selection at this region is that recombination between EL and GY QTL is limited. This cluster of QTL mapped near the centromere where the recombination rate is generally low. The region (*nc013–bnlg1740*) on chromosome 6, however, where a GY QTL and two EL QTL were in coupling linkage, should have benefited the increase in GY by selection on EL in the BSLE long-ear sub-population. This region may be a significant cause of the positive correlation between EL and GY.

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Table 1. Means, ranges, and broad-sense heritabilities (h^2) for five maize ear traits evaluated on the parents and generations of SE-40×LE-37 in 2000 and 2001.

	EL		GY		KWT		KRN		KD	
Parent or generation	$\bar{x}$ †	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range
2000 (plant basis)	cm		g plant^{-1}		g		no.		cm	
SE-40	8.3	5.1–11.8	NA‡	NA	NA	NA	18.4	14–24	0.68	0.40–0.85
LE-37	22.5	17.1–27.0	NA	NA	NA	NA	12.5	10–14	NA	NA
F_1	22.1	18.6–24.4	176	92–271	66	44–82	17.6	14–22	0.79	0.60–1.05
F_2 (188 plants)	18.8	11.1–23.9	93	32–144	52	34–99	16.7	12–22	0.66	0.45–0.90
h^2 §	0.65		0.53		0.01		0.58		0.53	
2001 (entry-mean basis)										
SE-40	8.2	–	38	–	69	–	15.0	–	0.62	–
LE-37	21.9	–	NA	–	NA	–	9.0	–	NA	–
F_1	23.1	–	229	–	86	–	16.5	–	0.85	–
$F_{2:3}$ (188 lines)	17.0	12.9–19.8	92	32–125	68	47–90	14.7	11.8–17.5	0.62	0.30–0.78
h^2 [CI] ¶	0.94	[0.93–0.95]	0.87	[0.83–0.90]	0.76	[0.70–0.81]	0.94	[0.92–0.95]	0.90	[0.88–0.92]
$\sigma_g^2 \pm$ SE	2.0 ± 0.2		216 ± 26		36 ± 5		1.1 ± 0.1		0.005 ± 0 #	
$\sigma_{ge}^2 \pm$ SE	0.5 ± 0.0		132 ± 8		46 ± 3		0.3 ± 0.0		0.002 ± 0	
F_2–$F_{2:3}$ regression										
h^2 [CI] ††	0.37	[0.30–0.44]	0.39	[0.31–0.48]	0.22	[0.12–0.32]	0.33	[0.28–0.39]	0.31	[0.21–0.41]

† Means estimated from ≈120 plants of SE-40, LE-37, and their F_1 in 2000, and triplicate entries in 2001.
‡ Not available or estimated from small number of plants.
§ h^2 on plant basis (Weber and Moorthy, 1952).
¶ h^2 and 95%-confidence interval [CI] on progeny-mean basis (Knapp et al., 1985).
# Standard error (SE) of zero is due to rounding.
†† h^2 and 95%-CI estimated from linear regression of $F_{2:3}$-progeny means onto F_2 plants.

Table 2. Phenotypic correlation coefficients (r_ps) among 188 F_2 plants (above diagonal) and, below diagonal, the r_ps (upper value) and genotypic correlation coefficients (lower value) among the $F_{2:3}$–progeny means for five traits evaluated in SE-40×LE-37 maize population.

Trait	EL	GY	KWT	KRN	KD
EL		0.63**	0.30**	–0.25**	–0.18*
(cm)					
GY	0.25**		0.61**	0.07	0.26**
(g plant^{-1})	0.22(0.10)†				
KWT	0.02	0.03		–0.19*	0.24**
(g)	0.02(0.07)	–0.01(0.07)			
KRN	–0.25**	0.43**	–0.28**		0.37**
(no.)	–0.28(0.11)	0.44(0.15)	–0.32(0.13)		
KD	–0.24**	0.70**	0.05	0.57**	
(cm)	–0.29(0.11)	0.73(0.24)	0.02(0.07)	0.61(0.19)	

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.
† Approximate standard error of genotypic correlation coefficient.

Table 3. Number of QTL detected for four maize ear traits in each generation-environment combination, consistency of detection across environments and generations, and the genotypic variation explained by QTL in the $F_{2:3}$ mean environment.

	QTL detected											
	F_2	$F_{2:3}$										
			Environment (Env.)					Mean environment and				
Trait	Ames	Total	Ames	Ankeny	Craw-fordsville	Lewis	Mean	≥ 2 Env. †	≥ 3 Env.	all 4 Env.	F_2 Env.	σ_g^2 explained ‡
	no.											%
EL	9	26	11	14	12	10	16	11	8	4	5	75
GY	3	6	4	2	2	2	3	2	1	1	1	41
KRN	10	23	9	7	14	10	12	10	4	1	6	67
KD	7	19	10	6	8	5	6	4	2	0	4	51
Total:	29	74	34	29	36	27	37	27	15	6	16	

† Number of QTL consistently identified in the mean environment and any two or more environments used to evaluate $F_{2:3}$ progeny.

‡ Genotypic variation explained by the multiple-QTL model adjusted for degrees of freedom. σ_g^2 explained = σ_p^2 explained / h^2.

Table 4. Summary of QTL positions, genetic effects, and consistency (†) of detection between $F_{2:3}$ progeny and their "parental" F_2 plants in the SE-40×LE-37 maize population.

	$F_{2:3}$ Progeny							F_2 Plant						
			Additive		Dominance					Additive		Dominance		
Chrom.	Pos. ‡	Locus	Effect §	Partial r^2 ¶	Effect	Partial r^2	Gene action #	Pos.	Locus	Effect	Partial r^2	Effect	Partial r^2	Gene action
							Grain yield (genetic effects in g plant^{-1})							
2								14	*bnlg2277*	4	1.2	12**	4.8	OD
3								162	*NPI257*	–3	1.2	8**	2.9	OD
5	100	*ISU77*	–12**	26.8	8**	6.8	OD	100	*ISU77*	–14**	18.4	14**	8.7	D
6	122	*UMC160A*	4**	2.9	3	0.7	OD							
10	20	*phi050*	2	0.6	7**	4.4	OD							
σ_p^2 explained ††			36%							34%				
							Kernel-row number (genetic effects in no.)							
1								42	*UMC157*	–0.6**	3.8	0.5*	1.3	D
1	62	*NPI234*	–0.7**	16.2	0.1	0.2	PD							
1								102	*ISU98A*	–0.9**	6.8	–0.1	0.1	A
1	212	*tb1isussr*	–0.4**	3.9	0.2	0.7	D	226	*phi265454*	–1.2**	11.5	–0.2	0.1	A

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

† QTL that share a row are considered the same based on overlapping 20-cM intervals.

‡ Position of highest LOD value in cM from the distal end of the short chromosome arm.

§ Positive and negative (–) values indicated an allele from LE-37 or SE-40, respectively, increased the trait's phenotype.

¶ Phenotypic variation (%) explained by the genetic effect after accounting for all other effects in the multiple-QTL model.

Level of dominance ($2d/a$ for $F_{2:3}$ and d/a for F_2) partitioned by published criterion (Stuber et al., 1987). A = additive (0–0.20); PD = partial-dominance (0.21–0.80); D = dominance (0.81–1.20); and OD = over-dominance (> 1.21).

†† Phenotypic variation explained by the multiple-QTL model adjusted for degrees of freedom.

Table 4. (cont.)

	$F_{2:3}$ Progeny							F_2 Plant						
			Additive		Dominance					Additive		Dominance		
Chrom.	Pos.	Locus	Effect	Partial r^2	Effect	Partial r^2	Gene action	Pos.	Locus	Effect	Partial r^2	Effect	Partial r^2	Gene action
1	246	*bnlg1055*	-0.3**	2.0	0.0	0.0	PD							
2	4	*bnlg1297*	-0.3**	3.8	0.3*	0.9	OD	0	*bnlg1297*	-0.6**	3.6	0.5*	1.2	D
3	158	*NPI257*	-0.3**	4.3	0.1	0.2	PD	152	*NPI212*	-0.7**	6.7	-0.1	0.0	A
4	94	*mmc0321*	0.4**	4.6	-0.1	0.1	PD	94	*mmc0321*	0.5**	2.4	0.4	0.7	PD
5	94	*BNL10.06*	-0.5**	6.9	0.2	0.5	PD							
6								144	*bnlg1740*	-0.7**	3.6	0.0	0.0	A
7								42	*phi034*	0.6**	3.4	0.1	0.1	A
7	100	*umc1412*	-0.2**	1.5	0.3**	1.3	OD							
8	16	*umc1974*	0.2*	1.2	0.0	0.0	A	30	*umc1360*	0.6**	3.3	-0.2	0.1	PD
9	48	*phi022*	-0.4**	5.4	-0.1	0.1	PD							
9	98	*umc1657*	-0.2**	1.4	0.1	0.2	D							
10	88	*phi323152*	-0.3**	3.3	0.1	0.3	D	78	*bnlg1360*	-0.8**	5.4	0.2	0.2	PD
σ_p^2 explained			---------- 63% ----------							---------- 47% ----------				
---------- Kernel depth (genetic effects in cm) ----------														
1								170	*bnlg1025*	0.03**	2.7	0.02	1.2	D
1	220	*ISU6*	-0.01*	1.2	0.03**	2.4	OD	208	*tb1isussr*	-0.04**	5.4	0.00	0.0	A
2								22	*bnlg2277*	-0.03**	4.8	0.03*	2.2	D
2	46	*NPI287*	-0.03**	6.2	0.02*	1.6	OD							

Table 4. (cont.)

	$F_{2:3}$ Progeny							F_2 Plant						
			Additive		Dominance					Additive		Dominance		
Chrom.	Pos.	Locus	Effect	Partial r^2	Effect	Partial r^2	Gene action	Pos.	Locus	Effect	Partial r^2	Effect	Partial r^2	Gene action
3	74	*bnlg602*	–0.01	0.6	0.03**	3.2	OD							
3	142	*BNL6.16*	–0.03**	8.0	–0.01	0.2	PD	158	*NPI257*	–0.04**	7.9	–0.02	0.5	PD
5	92	*BNL10.06*	–0.06**	19.4	0.02*	1.3	PD	90	*BNL10.06*	–0.03**	4.1	0.04*	2.4	D
5	180	*UMC68*	–0.02**	4.2	0.00	0.0	A	178	*UMC68*	–0.03**	3.6	0.00	0.0	A
10								60	*bnlg2190*	–0.02**	2.5	–0.02	1.0	D
σ_p^2 explained			---------- 46% ----------							---------- 29% ----------				

Table 5. Summary of digenic epistatic interactions for three maize ear traits, identified in the F_2 and $F_{2:3}$ generations of the SE-40×LE-37 population, that when added to the multiple-QTL model increased the percent of phenotypic variation (σ_p^2) explained.

Trait–Generation	Chromosomes	Marker-locus pair †	Interaction type ‡	Increase of σ_p^2 explained §
				(percentage points)
GY–F_2	2 × 8	*bnlg1297*(ns) × *ISU91*(ns)	*a*×*a*, *d*×*d*	4
GY–$F_{2:3}$	1 × 2	*ISU6*(**) × *ISU109*(ns)	*a*×*a*	4
	2 × 5	*bnlg1297*(*) × *phi330507*(**)	*d*×*a*, *d*×*d*	4
	5 × 9	*bnlg609*(ns) × *umc1691*(ns)	*a*×*d*	1
			All GY–$F_{2:3}$:	14 ¶
KRN–F_2	9 × 9	*umc1691*(**) × *umc1657*(ns)	*d*×*a*	4
	6 × 7	*bnlg1371*(ns) × *bnlg2132*(ns)	*d*×*d*	3
			All KRN–F_2:	6
KRN–$F_{2:3}$	1 × 3	*UMC164*(ns) × *bnlg2241*(ns)	*a*×*d*	2
KD–F_2	1 × 4	*CSU164*(ns) × *bnlg2291*(ns)	*a*×*d*	5
	5 × 8	*UMC68*(*) × *bnlg2181*(*)	*d*×*a*, *d*×*d*	3
			All KD–F_2:	10

† Locus pair with a significant epistatic effect(s). *, **, ns, indicate the additive (*a*) or dominance (*d*) effect of a marker locus was significant at the 0.05 or 0.01 probability levels, or non-significant, respectively.

‡ Type of interaction significant in the multiple-regression model.

§ Difference in adjusted-R^2 (x 100) values between the multiple-regression model with marker loci nearest each main-effect QTL and the marker-locus pair involved in each interaction, and the model with only marker loci nearest each main-effect QTL.

¶ Increase of σ_p^2 explained by adding all marker-locus pairs and their significant interactions to the multiple-QTL model.

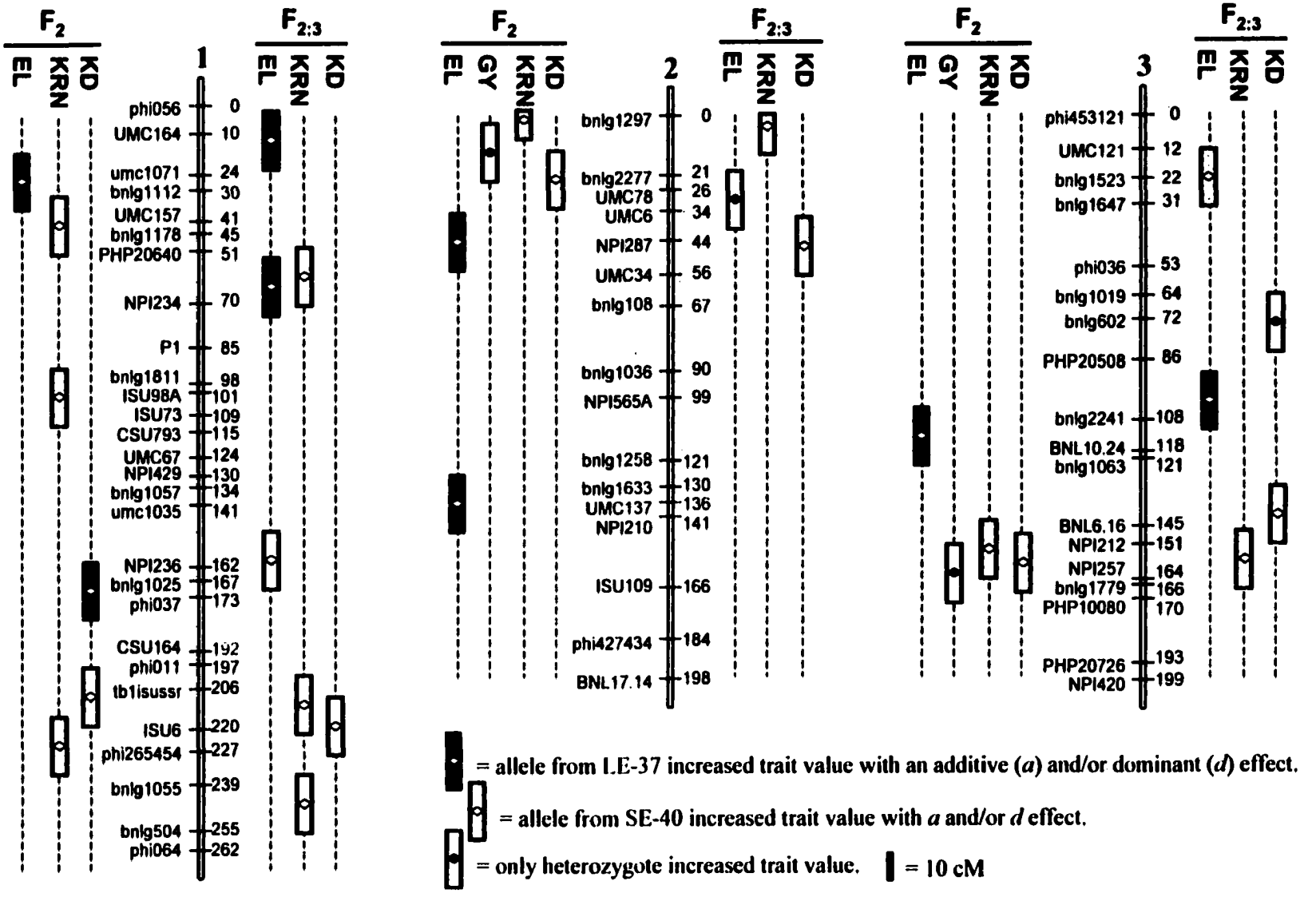
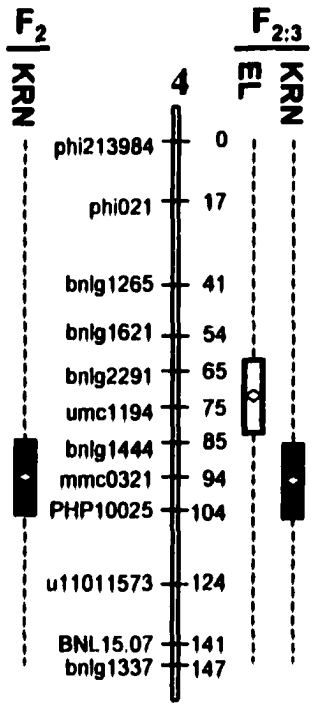
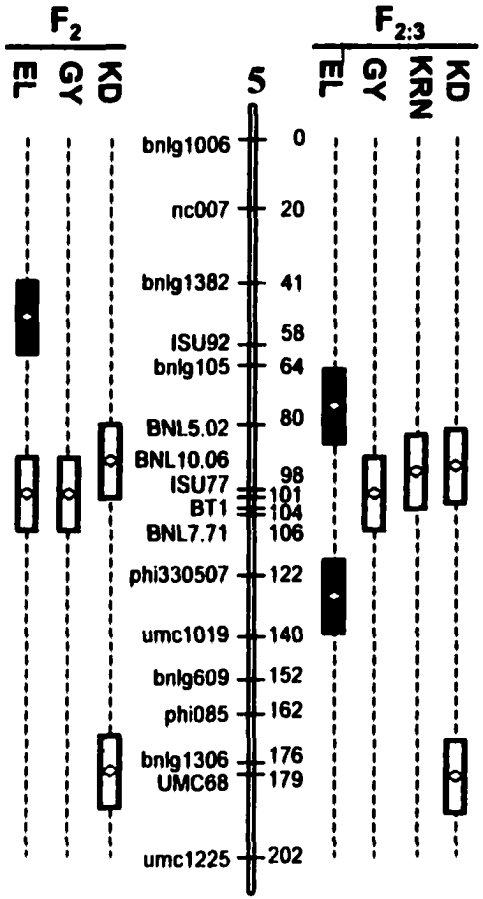


Figure 1. Distribution of QTL detected among F_2 plants and their $F_{2:3}$ progenies from the SE-40×LE-37 maize population.





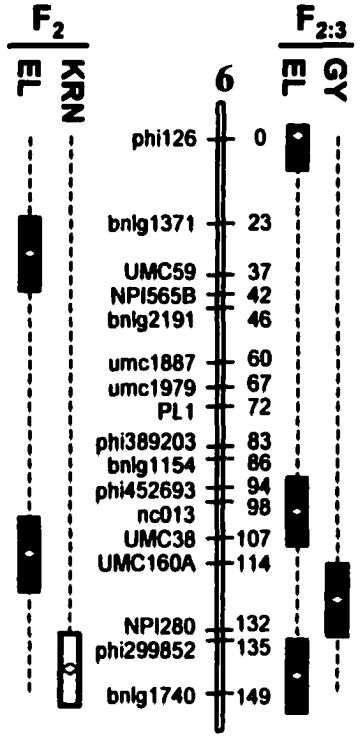


Figure 1. (cont.)

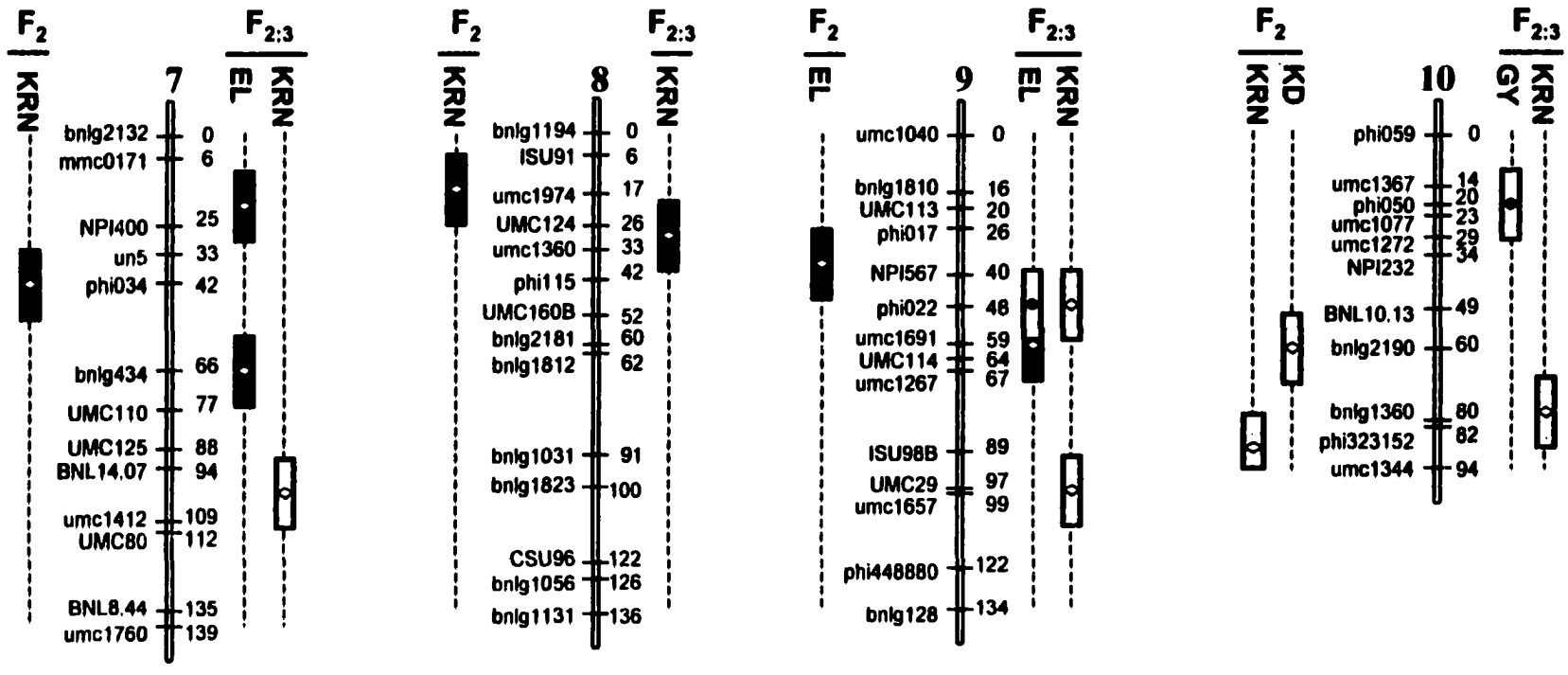


Figure 1. (cont.)

Chapter 3 Appendix – Table 1. Summary of KWT QTL positions, genetic effects, and consistency (†) of detection between $F_{2:3}$ progeny and their "parental" F_2 plants in the SE-40×LE-37 maize population.

	$F_{2:3}$ Progeny							F_2 Plant						
			Additive		Dominance					Additive		Dominance		
Chrom.	Pos. ‡	Locus	Effect §	Partial r^2 ¶	Effect #	Partial r^2	Gene action #	Pos.	Locus	Effect	Partial r^2	Effect	Partial r^2	Gene action
1	214	*ISU6*	3**	8.2	0	0.0	A	224	*phi265454*	4**	8.3	1	0.4	PD
3	78	*bnlg602*	–2**	4.6	0	0.0	A							
3	140	*BNL6.16*	–3**	7.9	2	0.8	D							
4	98	*mmc0321*	–3**	5.7	0	0.0	A							
5	84	*BNL5.02*	–2**	2.0	0	0.0	A	100	*ISU77*	–6**	16.6	3*	2.3	PD
5	176	*bnlg1306*	–2**	3.1	0	0.1	PD							
6	36	*UMC59*	2**	3.5	1	0.1	PD							
6								126	*NPI280*	3**	5.1	1	0.2	PD
7	136	*BNL8.44*	1**	2.4	2*	1.4	OD							
9	60	*umc1691*	3**	7.9	0	0.1	PD							
σ_p^2 explained ††			---------- 43% ----------							---------- 26% ----------				

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

† QTL that share a row are considered the same based on overlapping 20-cM intervals.

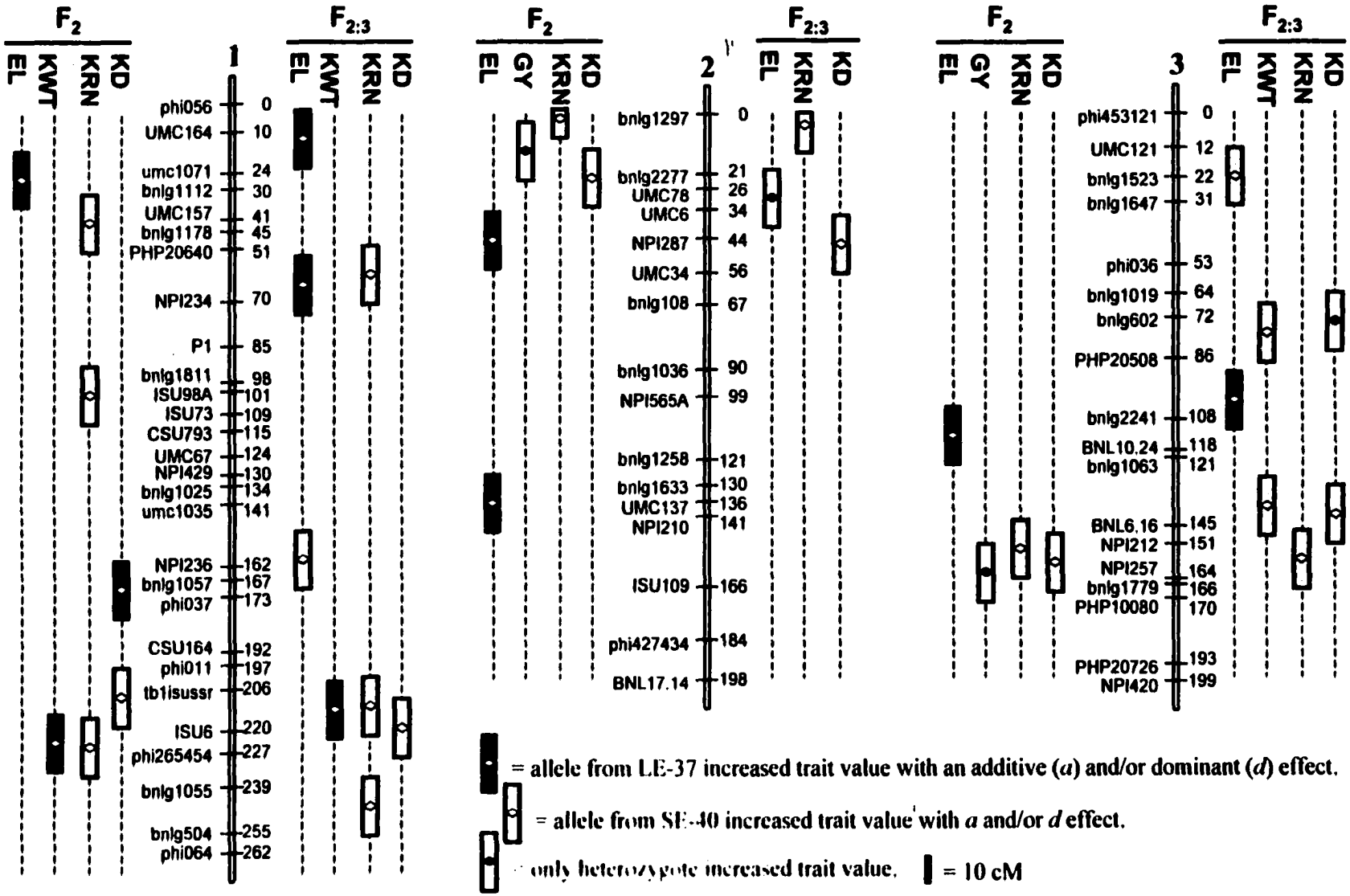
‡ Position of highest LOD value in cM from the distal end of the short chromosome arm.

§ effects in g 300-kernels^{-1} Positive and negative (–) values indicated an allele from LE-37 or SE-40, respectively, increased the trait's phenotype.

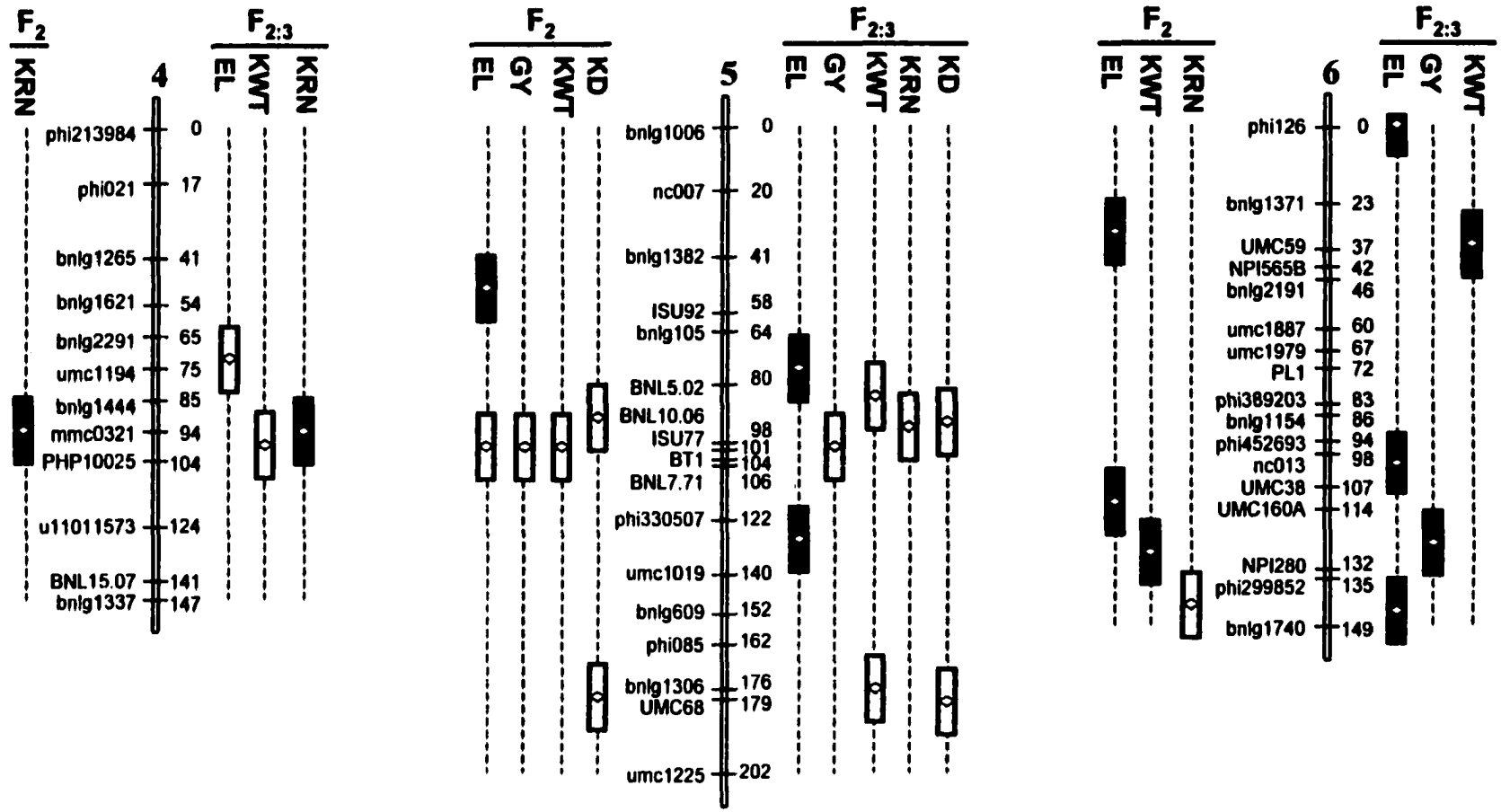
¶ Phenotypic variation (%) explained by the genetic effect after accounting for all other effects in the multiple-QTL model.

Level of dominance ($2d/a$ for $F_{2:3}$ and d/a for F_2) partitioned by published criterion (Stuber et al., 1987). A = additive (0–0.20); PD = partial-dominance (0.21–0.80); D = dominance (0.81–1.20); and OD = over-dominance (> 1.21).

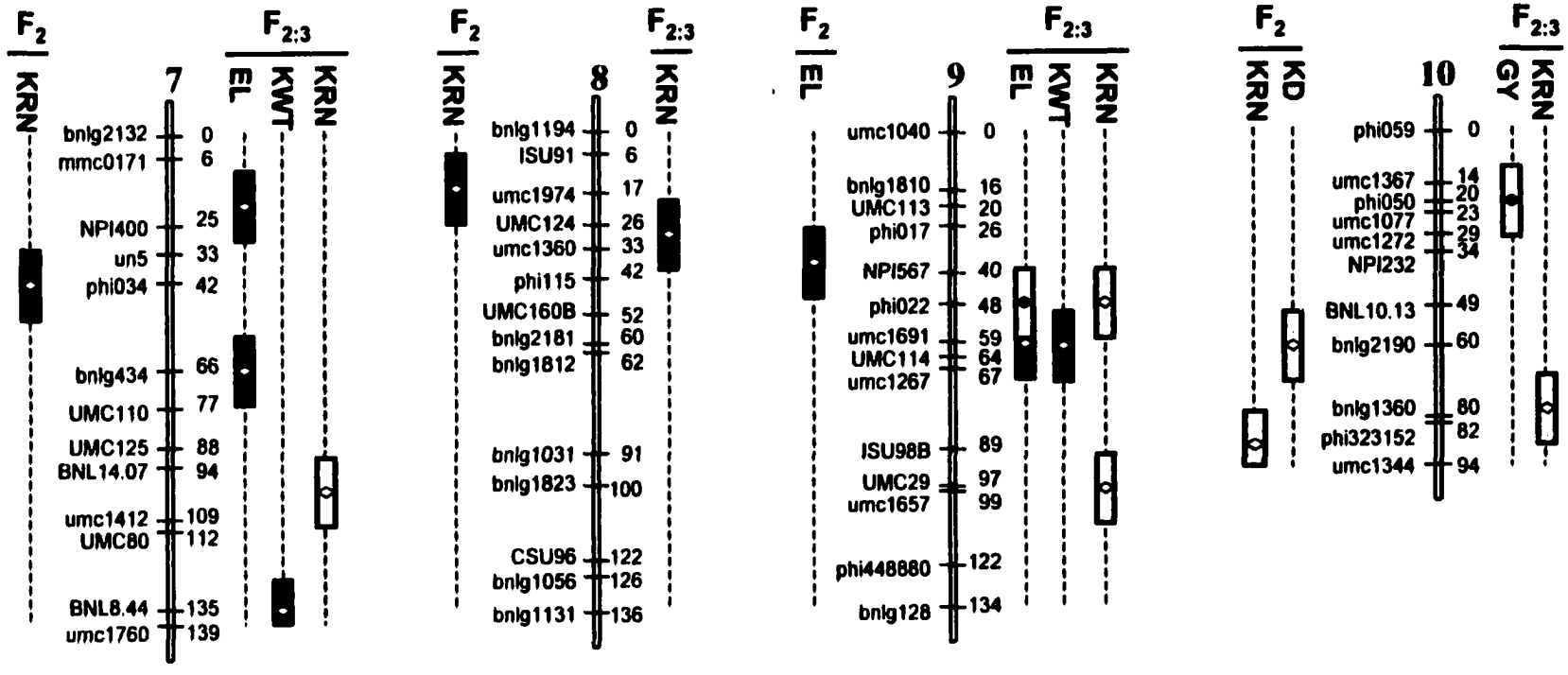
†† Phenotypic variation explained by the multiple-QTL model adjusted for degrees of freedom.



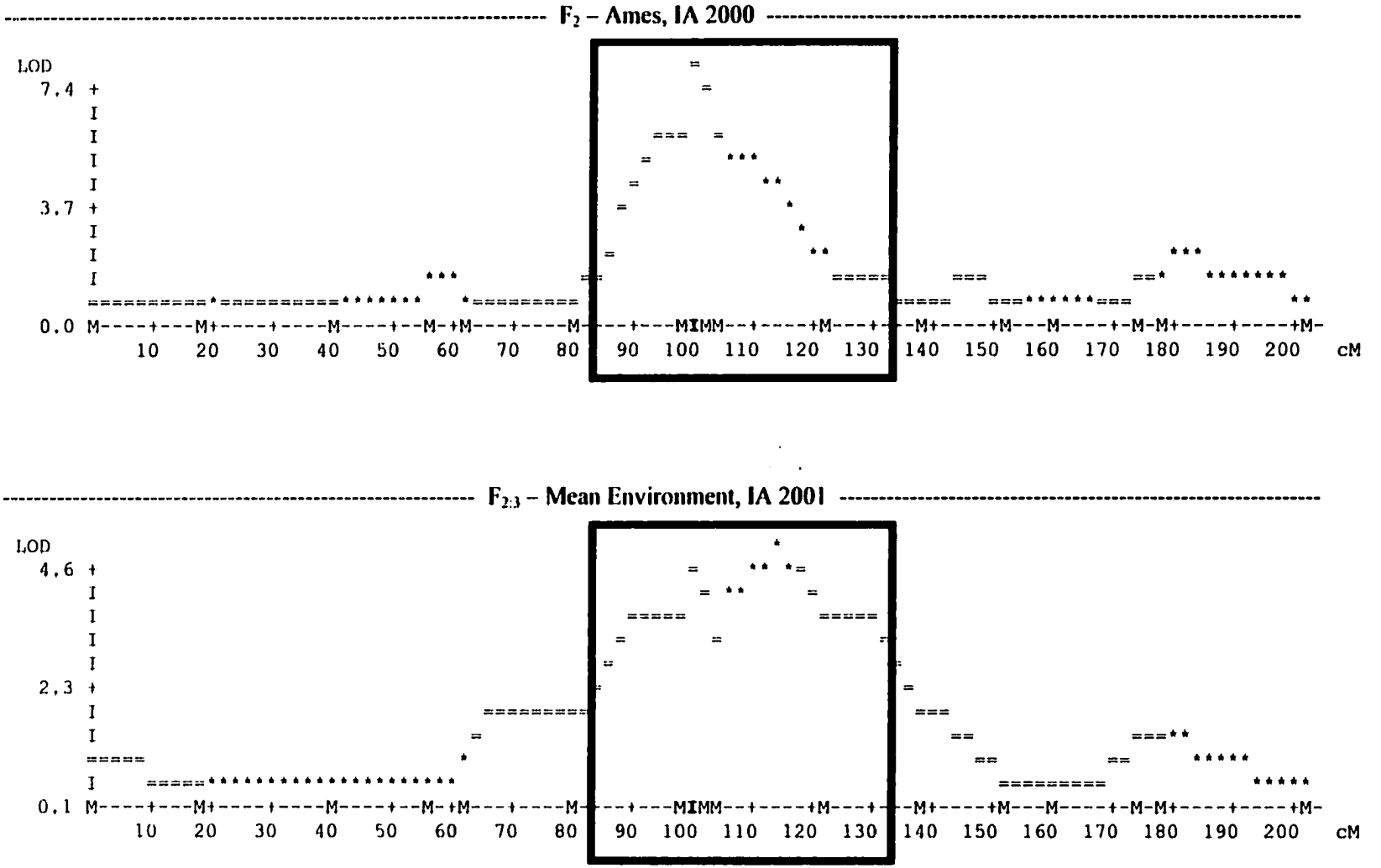
Chapter 3 Appendix - Figure 1. Distribution of KWT QTL relative to other ear trait QTL segregating among $F_{2:3}$ progenies and their parental F_2 plants detected in the SE-40×LE-37 maize population.



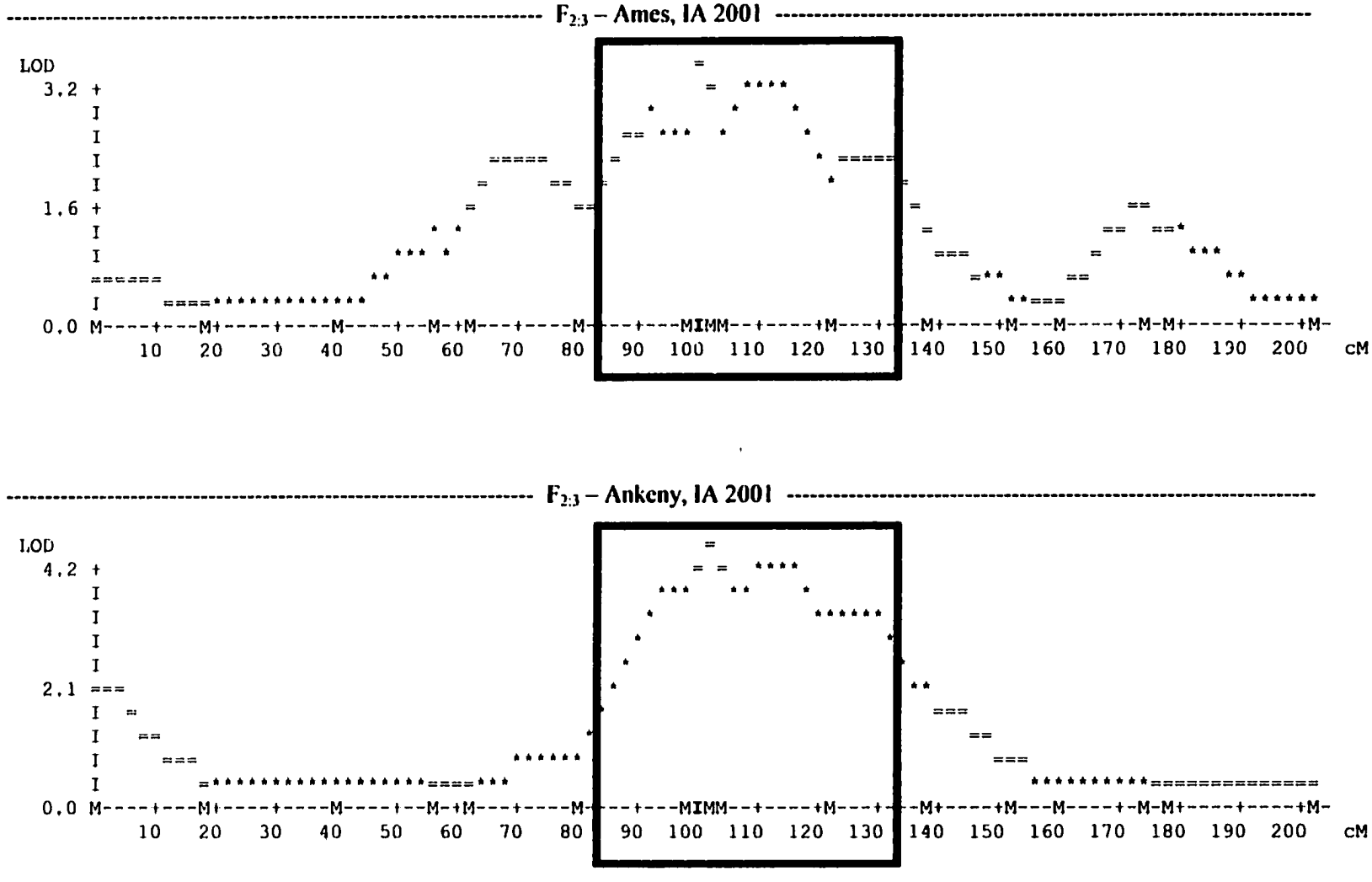
Chapter 3 Appendix - Figure 1. (cont.)



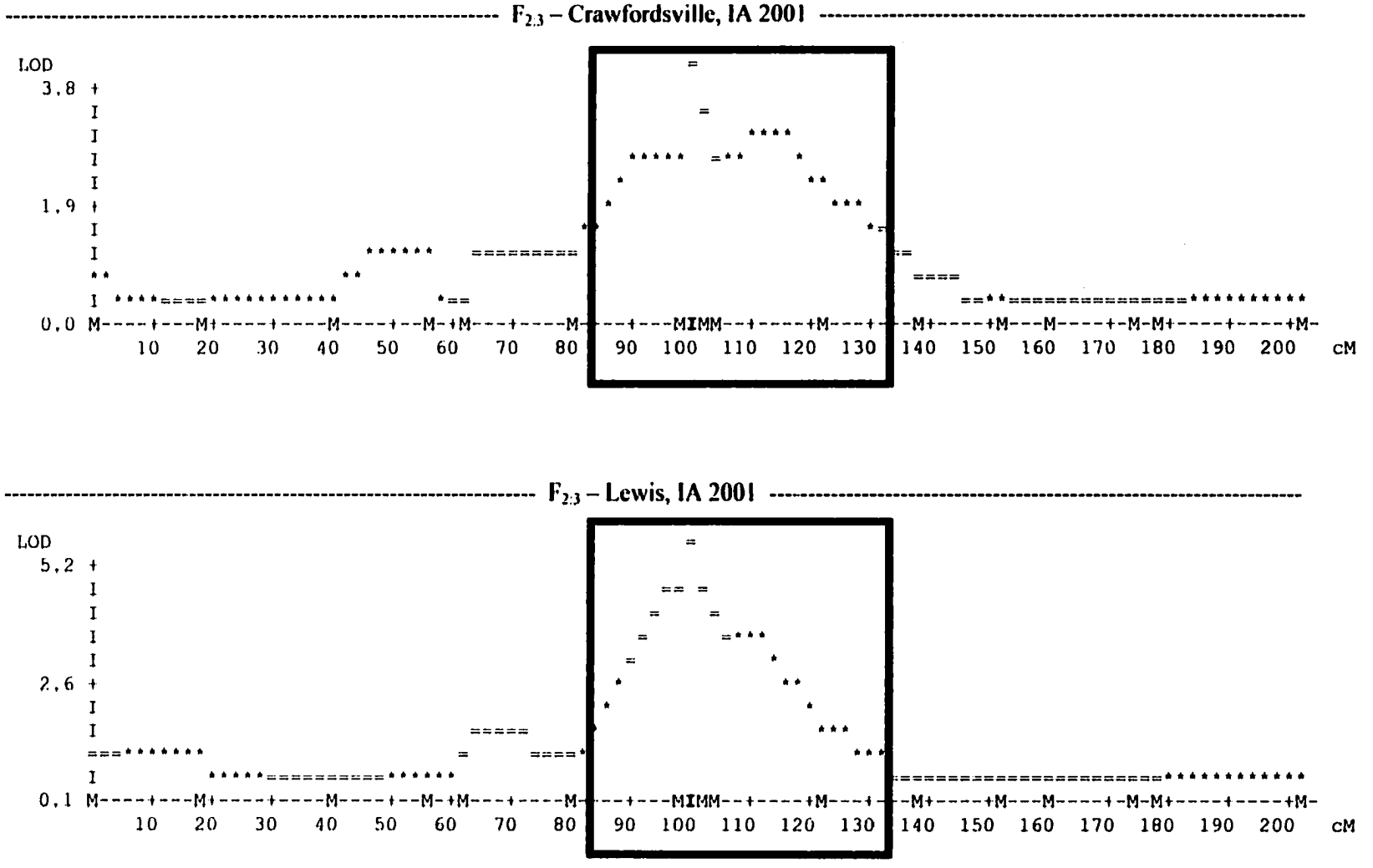
Chapter 3 Appendix - Figure 1. (cont.)



Chapter 3 Appendix – Figure 2. Chromosome 5 LOD scans (at 2 cM intervals), from the F_2, $F_{2:3}$ mean, and four $F_{2:3}$ individual environments, using all marker loci (M) as cofactors in composite interval mapping with PLABQTL (Utz and Melchinger, 1996). "*" indicated LE-37 allele increased GY, and "=" indicated SE-40 allele increased GY. LOD threshold for declaring QTL significant was 2.5. Region enclosed within box is area of interest. Marker locus *ISU77* indicated by the bold "**I**."



Chapter 3 Appendix – Figure 2 (cont.)



Chapter 3 Appendix – Figure 2 (cont.)

CHAPTER 4.
GENERAL CONCLUSION

General Discussion

The SE-40×LE-37 population, extensive phenotype evaluation, and statistical procedures used for the investigations presented herein allowed more QTL to be mapped for EL, KRN, and KD compared with prior QTL mapping studies. Development of SE-40 and LE-37 by divergent selection for EL probably benefited QTL detection for EL, and traits with divergent correlated responses to EL selection. The divergence of the parent phenotypes was exhibited at the genetic level. Eighty percent of the alleles increasing EL originated from LE-37. SE-40 had the higher parental value for KRN and KD, and provided 80% or more of the alleles that increased these traits. Exclusive credit for increased QTL detection cannot be attributed to the divergent parents because other factors beneficial to QTL identification also were improved.

In the F_2, nine QTL were mapped for EL, 10 for KRN, seven for KD, and three for GY. In the $F_{2:3}$ mean environment, the number of QTL was 16 for EL, 12 for KRN, six for KD, and three for GY. The 16 QTL in the $F_{2:3}$ explained 70% of the EL variation. The 12 QTL for KRN explained 63% and the six for KD explained 46% of the phenotypic variation among $F_{2:3}$ progenies. Three QTL for GY in the $F_{2:3}$ explained only 36% of the variation. Epistatic interactions increased the amount of phenotypic variation explained for KRN, KD, and GY. Three pair of epistatic marker loci in the $F_{2:3}$ cumulatively increased the amount of GY variation explained by 14 percentage points. Epistatic effects were identified for EL, and were consistent across three or more $F_{2:3}$ individual environments, but failed to explain additional variation when added to the model containing multiple main-effect QTL. To understand the true impact of epistatic effects they may need to be evaluated in a constant genetic background, such as near isogenic lines.

Additive genetic effects were predominant for EL, KRN, and KD QTL in both generations. The magnitude of effects was not equal between generations for EL and KRN. Additive effects in the F_2 ranged from 0.4 to 1.3 cm, and in the $F_{2:3}$ from 0.3 to 0.7 cm for EL. For KRN, the range of additive effects was 0.5 to 1.2 kernel-rows in the F_2, and 0.2 to 0.7 kernel-rows in the $F_{2:3}$. KD QTL had similar additive effects in each generation and the average effect was 0.03 cm. The difference in the magnitude of effects across generations for EL and KRN was attributed to phenotype estimates. Additive effects seemed less important than dominance effects for GY variation. Dominance effects

were significant for all GY QTL in both generations except for a QTL on chromosome 6 in the $F_{2:3}$. The level of dominance for all but one GY QTL was in the over-dominant range.

Confidence that QTL from SE-40×LE-37 were not false-positive detections was provided by three validation methods: 1) identification of QTL in multiple environments, 2) in successive generations, and 3) in other populations. More than 67% of the QTL (EL, KRN, KD, and GY) identified in the $F_{2:3}$ mean environment were detected at two or more individual environments, and 33% or more QTL were identified in at least three environments. Twenty-five percent of the EL QTL were detected at the four $F_{2:3}$ environments. All QTL identified at more than one environment had alleles increasing trait values from the same parent, and the magnitude of the effects at these loci was relatively stable across environments.

Validation of QTL by comparing QTL positions in the F_2 and $F_{2:3}$ generations was informative in SE-40×LE-37. Forty-three percent of the EL, GY, KRN, and KD QTL coincided between generations. KRN had the most QTL (6) identified in both generations and GY (1) the least. In general, the number of coincidental QTL followed the trend of progeny-mean heritabilities. Validation by comparing QTL positions across successive generations should compliment other validation methods. This method has received little use in maize investigations. Validating QTL by a successive-generation method requires less research expenditures than other methods and may be completed during the seasons of progeny development. This method can easily be implemented in experimental designs that derive progeny from a single plant (e.g., F_2– or F_3–derived lines, RILs, and AILs).

Several QTL detected in the $F_{2:3}$ of SE-40×LE-37, were previously identified in other populations. Seven EL QTL seemed to map to the same genetic positions of EL QTL identified in the $F_{2:3}$ and/or $F_{6:7}$ generations of a Mo17×H99 population (Austin and Lee, 1998). A KRN QTL on chromosome 4 showed impressive consistency, and was identified in both generations of SE-40×LE-37 and Mo17×H99 (Austin and Lee, 1998), and the among $F_{2:4}$ lines of B73×Mo17 (Beavis et al., 1994). The GY QTL on chromosome 5 was identified in a B73×Mo17 population (Stuber et al., 1992; Graham et al., 1997), and the GY QTL on chromosome 6 was found in all generation-environment combinations used to evaluate a Mo17×H99 population (Veldboom and Lee, 1996; Austin and Lee, 1998). The detection of these QTL across several populations indicates their significant role in affecting trait variation.

Mapping QTL in SE-40×LE-37 provided genetic information to aid the understanding of the EL phenotype and trait correlations. It was hypothesized that the number of cupules in a 5-cm

interval of EL may partially explain EL variation, and indicate if an increase in EL was due to an increase in the distance between cupules or the number of cupules. For ease of phenotype collection, cupules in a 5-cm interval of EL was estimated by K/5CM. EL and K/5CM were only moderately correlated ($r_p \approx -0.25$), and of the 12 QTL for K/5CM detected in the $F_{2:3}$ of SE-40×LE-37, only one QTL coincided with an EL QTL. These results indicated that K/5CM had little value as a descriptive component of EL. However, these results may have been caused by K/5CM being a poor estimate of cupules per 5 cm, and may have differed if cupules per 5 cm was estimated directly.
Direct measurement of cupules per 5 cm would be laborious because cupules are not easily counted from the rachis. The glumes remaining on a rachis stripped of grain obscure the visualization and accurate count of cupules. An alternative to measuring cupules on the ear may be to estimate cupules from the tassel, where they are not obscured, and relate the distance between cupules to the ear. This may be a plausible alternative because of the homologies between the ear and tassel architectures (Anderson, 1944).

The QTL positions of EL, GY, KRN, and KD were used to determine if a genetic basis for correlations between these traits could be identified. QTL positions and the parental origin of alleles that increased trait values agreed with the direction of r_gs in SE-40×LE-37, and were in accordance with the inability to indirectly increase GY by selection on EL in the BSLE experiment (Hallauer et al., 2003). The magnitude of r_gs was generally explained by the frequency of QTL located at the same genetic position or in linkage disequilibrium. The resolution of the SE-40×LE-37 genetic map did not allow definite causes (pleiotropy and linkage) of genetic correlations to be determined. The coincidence and linkage of QTL provided some evidence for the causes of trait correlations.

QTL positions provided information regarding the failure to increase GY by selection for EL in the BSLE long-ear sub-population. A cluster of QTL near the centromere of chromosome 5, where two EL QTL were linked in repulsion to a QTL that explained 31% of the GY variation among $F_{2:3}$ progenies, may have had a significant role in the failure of BSLE experiment to increase GY. The positive correlation between EL and GY observed in SE-40×LE-37 and generally observed in other maize populations (Hallauer and Miranda, 1988) may be due to a region on chromosome 6 where a GY QTL and two EL QTL were in coupling linkage.

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APPENDIX A

SUPPLEMENTAL INFORMATION ON THE STATISTICAL ANALYSES OF PHENOTYPE DATA

The following information was included as an appendix to provide the reader with information pertaining to the statistical analyses of the phenotypic data, collected from the F_2 plants and $F_{2:3}$ progeny from the cross SE-40×LE-37, that was not presented in the main body of the dissertation.

Data Analyses – F_2 Generation

Data for 12 traits was obtained at Ames, IA in 2000 from 189 F_2 plants from the mating of SE-40 with LE-37. Data was also collected from individual plants of the inbred parents, SE-40 and LE-37, and plants of the F_1 generation. One F_2 plant was dropped from the analysis for reasons described in the following section. The mean and variance was computed for each trait within each source of plants (SE-40, LE-37, F_1, and F_2). The variances were used to calculate broad-sense heritabilities (h^2). Four formulas were used to estimate h^2. Each formula obtains the phenotypic variance from the variance among F_2 plants, but the formulas are unique in their method of obtaining an estimate of the environmental variance, which was estimated by plants from the homogenous source(s) (inbred parents and their F_1).

$$h^2 = \frac{\sigma^2_{F_2} - \sigma^2_{F_1}}{\sigma^2_{F_2}}$$, described by Burton (1951);

$$h^2 = \frac{\sigma^2_{F_2} - \sqrt{\sigma^2_{P_1}\,\sigma^2_{P_2}}}{\sigma^2_{F_2}}$$, described by Mahmud and Kramer (1951);

$$h^2 = \frac{\sigma^2_{F_2} - \sqrt[3]{\sigma^2_{P_1}\;\sigma^2_{P_2}\;\sigma^2_{F_1}}}{\sigma^2_{F_2}}$$, described by Weber and Moorthy (1952);

$$h^2 = \frac{\sigma^2_{F_2} - \sqrt[4]{\sigma^2_{P_1}\;\sigma^2_{P_2}\;2\,\sigma^2_{F_1}}}{\sigma^2_{F_2}}$$, described by Weber and Moorthy (1952);

where

$\sigma^2_{F_2}$ = the variance among the 188 F_2 plants, and

$\sigma^2_{F_1}$ = the variance among F_1 plants from SE-40×LE-37,

$\sigma^2_{P_1}$ = the variance among plants of SE-40, and

$\sigma^2_{P_2}$ = the variance among plants of LE-37.

Data Analyses – $F_{2:3}$ Generation

Trait data was obtained from the $F_{2:3}$ progeny evaluated in a 200-entry experiment replicated twice at four Iowa environments in 2001. The experiment consisted of 189 $F_{2:3}$ lines and 11 check entries (three entries each of SE-40, LE-37, SE-40×LE-37, and one entry of (SE-40×LE-37)×SE-40, and (SE-40×LE-37)×LE-37). The experiment was randomized to a row(tier)–column lattice design [10 tiers and 20 columns] using Alphagen, a computer program developed by the Scottish Agricultural Statistics Service. Entry 186 [(SE-40×LE-37)-F1#2-251] was dropped from analyses of the experiment because data on the morphological trait glume color was not consistent across the F_2 and $F_{2:3}$ generations, indicating that the F_2 plant was not self-pollinated. Plot means were used for computation of statistics.

Analyses of data from individual environments was completed using the mixed model procedure (PROC MIXED) of SAS version 8.0 to obtain the entry least-square-means (lsmeans) adjusted for replication and intrablock (tier and column) effects, and the effective error mean square (EEMS) for each trait. Adjusted entry-lsmeans were computed from plot values adjusted for replication, tier and column effects by including those effects as random sources of variation in the mixed-linear model. The EEMS term was compiled as follows:

1) The standard errors (SE) for the difference between two adjusted entry-lsmeans means were computed for all possible combinations of entries.
2) Each SE was squared, multiplied by the number of replications in each mean, and divided by two.
3) The average of all values computed in step three was calculated.

The EEMS was the value obtained from step three (3). The effective error sum of squares (EESS) for each trait was obtained by multiplying the EEMS by its degrees of freedom (df).

Analyses of data combined across the four environments was completed by using the adjusted entry-lsmeans from each individual environment analysis. The analyses of variance were performed using a general linear model (PROC GLM) of SAS version 8.0.

The additive model was:

$$Y_{ij} = \mu + E_i + G_j + (GE)_{ij} + \text{Pooled Error},$$

where

Y_{ij} = the mean value of the j^{th} genotype at the i^{th} environment,
μ = overall mean,
E_i = effect of the i^{th} environment ($i = 1$ to 4),
G_j = effect of the j^{th} genotype ($j = 1$ to 199),
$(GE)_{ij}$ = effect of the interaction between the i^{th} environment with the j^{th} genotype, and
pooled error = calculated as described below.

Environments, Genotypes (entries), and the Environment×Genotype interaction (E×G) terms were considered random sources of variation. The sums of squares for Genotypes and E×G terms were partitioned into among $F_{2:3}$ progeny, among checks, and the orthogonal comparison (Table A.1). All partitioned terms were considered as random sources of variation except for the Checks term. Replications, Columns, and Tiers were included in Table A.1 to account for the total number of df, but were not part of the total variation because adjusted-entry lsmeans from the individual environments were used in the combined analysis rather than plot values.

To determine the significance of each source of variation *F*-tests were used. The Environment term was tested by the E×G interaction. The E×G interaction and its partitioned effects were also used to test the Genotype effect and the corresponding partitioned Genotype effects. The Pooled Error (pooled EEMS) term was used to test the E×G interaction and its partitioned effects. The pooled EEMS was computed by the summation of the EESS from the four individual environment analyses of variance; and dividing this sum by the pooled df from the error terms of the individual environment analyses.

Table A.1. Analysis of variance and expected mean squares for data combined across environments

Sources of variation	Degrees of freedom (df)	df	Expected mean squares	
Environments (E)	e-1	3	$\sigma^2_e + \sigma^2_{GE} + g\sigma^2_E$	
Replications (env) (R)	(r-1)e	4		
Columns [reps(env)] (C)	(c-1)re	72		
Tier [reps(env)] (T)	(t-1)re	152		
Genotypes (G)	g-1	198	$\sigma^2_e + \sigma^2_{GE} + e\sigma^2_G$	M
$F_{2:3}$ progeny (F)	f-1	187	$\sigma^2_e + \sigma^2_{FE} + e\sigma^2_F$	M
Checks (CH)	ch-1	10	$\sigma^2_e + \sigma^2_{CHE} + e\theta_{CH}$	M
F vs. CH	1	1	$\sigma^2_e + \sigma^2_{(F\ vs.\ CH)E} + e\sigma^2_{(F\ vs.\ CH)}$	M
E × G	(e-1) (g-1)	594	$\sigma^2_e + \sigma^2_{GE}$	M
E × F	(e-1) (f-1)	561	$\sigma^2_e + \sigma^2_{FE}$	M
E × CH	(e-1) (ch-1)	30	$\sigma^2_e + \sigma^2_{CHE}$	M
E × (F vs. CH)	(e-1) 1	3	$\sigma^2_e + \sigma^2_{(F\ vs.\ CH)E}$	M
Pooled Error (EEMS)	e{[(r-1)(g-1)]-[{(c-1)r}+{(t-1)r}]}	568	σ^2_e	M
Total	erg-1	1591		

Heritability, and phenotypic and genetic correlation coefficients were computed using sources of variation due to the $F_{2:3}$ progeny and the $F_{2:3}$ progeny×environment interaction. Heritability on a progeny-mean basis and the 95%-confidence interval of h^2 were computed for each trait as illustrated by Knapp et al. (1985). The h^2 equation was compiled by dividing the $F_{2:3}$ progeny×environment MS with the $F_{2:3}$ progeny MS, and subtracting that quotient from one.

Heritability among $F_{2:3}$ progeny was

$$h^2 = 1 - \frac{M_{21}}{M_{11}}$$

and the equation for the confidence interval of h^2 was

$$1 - \frac{1}{\frac{M_{11}}{M_{21}} F_{1-\alpha/2:df2,df1}} \leq h^2 \geq 1 - \frac{1}{\frac{M_{11}}{M_{21}} F_{\alpha/2:df2,df1}}$$

where

M_{21} = mean square for $F_{2:3}$ progeny×environment interaction,
M_{11} = mean square for $F_{2:3}$-progeny effect,
$F_{1-\alpha/2:df2,df1}$ = the critical F-value at 1-α/2 with df2 (561) and df1 (187),
df2 = degrees of freedom for the $F_{2:3}$ progeny×environment interaction, and
df1 = degrees of freedom for the $F_{2:3}$–progeny effect.

Regression of $F_{2:3}$–progeny means onto F_2–plant values was also used to determine the heritable portion of each trait's phenotypic variation. The F_2 values for each trait obtained at Ames, IA in 2000 were the regressor variables, and the $F_{2:3}$–progeny means estimated at four environments in 2001 and from the combined analysis of environments (mean environment) were the response variables for the estimation of the linear regression coefficient (b) and the 95%-confidence interval of b. The parent-offspring (F_2–$F_{2:3}$) h^2 was directly estimated by b when data from $F_{2:3}$ progeny were regressed onto F_2 plant data (Fernandez and Miller, 1985).

Phenotypic correlation coefficients between all traits for F_2 plants, $F_{2:3}$ progeny at the four individual environments, and the mean environment were calculated. Genotypic correlation coefficients and their approximate standard errors were computed, according to formulas presented by Mode and Robinson (1959), between traits analyzed in the mean environment of the $F_{2:3}$ progeny.

APPENDIX B

PHENOTYPE DATA OF F2 PLANTS GROWN IN 2000

Table B1. Performance of 188 F_2 plants from the SE-40×LE-37 maize population grown near Ames, IA, in 2000.

Entry No. †	Pedigree	EL‡	ED	CD	KD	KRN	K/5CM	KWT§	GY	PLTHT¶	TB#	Pgdd††	Sgdd
		cm				no.		g/300k	g plt^{-1}	cm	no.	gdd	
1	(SE-40/LE-37)-F1#2-002	19.3	3.8	2.7	0.6	14	13	54.3	84	200	4	763	763
2	(SE-40/LE-37)-F1#2-003	19.7	4.3	3.1	0.6	18	10	57.8	92	198	9	763	–
3	(SE-40/LE-37)-F1#2-004	18.7	3.5	2.4	0.6	14	15	43.5	79	198	6	775	775
4	(SE-40/LE-37)-F1#2-005	20.5	4.0	2.7	0.7	16	12	51.1	95	207	10	763	–
5	(SE-40/LE-37)-F1#2-006	18.9	3.9	2.8	0.6	14	12	50.4	59	213	5	775	–
6	(SE-40/LE-37)-F1#2-007	18.1	4.4	2.8	0.8	20	12	50.7	100	202	3	787	800
7	(SE-40/LE-37)-F1#2-008	20.6	4.1	2.9	0.6	16	11	55.8	98	198	5	743	763
8	(SE-40/LE-37)-F1#2-009	20.1	3.9	2.5	0.7	14	13	57.3	88	210	18	775	–
9	(SE-40/LE-37)-F1#2-010	21.3	4.0	2.9	0.6	14	11	73.1	103	226	11	775	–
10	(SE-40/LE-37)-F1#2-012	20.5	4.1	2.8	0.7	16	11	57.4	109	215	8	763	763
11	(SE-40/LE-37)-F1#2-013	13.0	4.0	2.6	0.7	20	13	39.0	50	181	13	775	–
12	(SE-40/LE-37)-F1#2-014	18.1	4.1	2.8	0.7	16	11	48.2	56	221	6	800	813
13	(SE-40/LE-37)-F1#2-017	19.9	4.4	3.0	0.7	18	12	64.3	127	206	6	763	775
14	(SE-40/LE-37)-F1#2-018	13.0	3.9	2.4	0.8	16	14	33.5	32	194	11	813	835
15	(SE-40/LE-37)-F1#2-019	20.8	3.8	2.6	0.6	18	11	37.8	59	216	14	813	–
16	(SE-40/LE-37)-F1#2-020	18.7	3.4	2.4	0.5	16	12	43.0	62	196	12	787	–
17	(SE-40/LE-37)-F1#2-021	20.1	3.7	2.5	0.6	16	13	55.9	106	199	10	734	734
18	(SE-40/LE-37)-F1#2-022	20.3	4.1	2.6	0.8	14	12	54.5	94	240	3	763	775
19	(SE-40/LE-37)-F1#2-023	16.2	3.6	2.4	0.6	14	13	46.4	61	206	10	775	–
20	(SE-40/LE-37)-F1#2-025	19.4	4.1	2.7	0.7	16	12	55.8	105	221	9	763	763
21	(SE-40/LE-37)-F1#2-026	20.0	3.8	2.7	0.6	16	11	50.9	78	230	9	823	–
22	(SE-40/LE-37)-F1#2-027	18.7	3.9	2.6	0.7	18	12	43.4	80	198	12	775	787
23	(SE-40/LE-37)-F1#2-028	18.4	4.6	3.0	0.8	18	13	54.3	111	212	12	743	763
24	(SE-40/LE-37)-F1#2-029	20.3	3.9	2.7	0.6	14	13	56.0	70	185	15	835	–
25	(SE-40/LE-37)-F1#2-032	23.2	3.6	2.4	0.6	14	10	61.9	99	212	7	800	800
26	(SE-40/LE-37)-F1#2-034	14.4	4.0	2.4	0.8	14	13	65.7	68	209	10	800	–
27	(SE-40/LE-37)-F1#2-036	17.2	3.9	2.3	0.8	18	12	46.0	73	209	13	800	800
28	(SE-40/LE-37)-F1#2-037	13.2	3.8	2.4	0.7	18	13	44.1	48	196	11	800	800
29	(SE-40/LE-37)-F1#2-038	20.7	4.2	2.7	0.8	16	12	66.0	120	205	8	743	743
30	(SE-40/LE-37)-F1#2-039	19.2	3.9	2.8	0.6	18	12	44.1	73	201	3	763	763

† Entry number of the $F_{2:3}$ line evaluated in experiment 19 in 2001.

‡ EL (ear length), ED (ear diameter), CD (cob diameter), KD (kernel depth), KRN (kernel-row number), and K/5CM (kernels per 5 cm) data were obtained from measurements on the primary ear of each F_2 plant.

§ KWT (kernel weight) was obtained by weighing 300 kernels, and GY (grain yield) by weighing all kernels from all seed-bearing ears harvested from each F_2 plant.

¶ PLTHT (plant height) was measured from the soil surface to the terminal node.

TB (number of secondary tassel branches) was obtained from each F_2 plant.

†† Pgdd and Sgdd = growing degree days (°C) when the plant showed male or female anthesis, respectively.

Table B1. (cont.)

Entry No.	Pedigree	EL	ED	CD	KD	KRN	K/5CM	KWT	GY	PLTHT	TB	Pgdd	Sgdd
		cm				no.		g/300k	g plt^{-1}	cm	no.	gdd	
31	(SE-40/LE-37)-F1#2-040	15.2	3.9	2.9	0.5	14	12	51.4	74	202	3	775	775
32	(SE-40/LE-37)-F1#2-041	21.1	4.1	2.8	0.7	18	10	55.1	112	225	6	734	734
33	(SE-40/LE-37)-F1#2-043	16.4	4.3	3.0	0.7	18	12	44.4	63	198	15	752	–
34	(SE-40/LE-37)-F1#2-044	17.2	4.0	2.8	0.6	16	12	47.0	67	211	13	813	–
35	(SE-40/LE-37)-F1#2-047	20.5	3.9	2.9	0.5	16	12	42.5	69	195	3	763	775
36	(SE-40/LE-37)-F1#2-049	18.7	4.3	3.1	0.6	20	11	55.6	96	200	9	743	743
37	(SE-40/LE-37)-F1#2-050	19.2	4.2	2.8	0.7	16	12	62.8	117	200	12	719	719
38	(SE-40/LE-37)-F1#2-051	19.2	4.0	2.6	0.7	18	10	72.9	97	206	–	752	763
39	(SE-40/LE-37)-F1#2-052	16.1	3.5	2.3	0.6	16	13	38.1	51	183	16	763	–
40	(SE-40/LE-37)-F1#2-053	16.4	3.9	2.8	0.6	18	12	39.8	52	200	12	823	862
41	(SE-40/LE-37)-F1#2-054	18.9	3.8	2.5	0.7	16	12	45.8	71	209	17	800	813
42	(SE-40/LE-37)-F1#2-055	19.7	4.0	2.7	0.7	14	12	87.9	90	221	5	752	752
43	(SE-40/LE-37)-F1#2-056	19.8	3.9	2.6	0.7	16	13	42.9	80	212	10	743	–
44	(SE-40/LE-37)-F1#2-057	17.0	3.9	2.9	0.5	16	14	40.1	65	220	8	775	775
45	(SE-40/LE-37)-F1#2-058	20.5	4.4	3.1	0.7	16	11	69.3	114	231	4	775	–
46	(SE-40/LE-37)-F1#2-059	18.2	3.4	2.5	0.5	16	13	36.0	52	192	10	800	823
47	(SE-40/LE-37)-F1#2-062	13.0	3.9	2.6	0.7	18	11	51.3	83	191	13	800	–
48	(SE-40/LE-37)-F1#2-063	15.4	4.1	2.7	0.7	18	12	53.9	87	223	8	775	800
49	(SE-40/LE-37)-F1#2-064	21.0	3.7	2.7	0.5	16	11	42.2	77	200	9	800	813
50	(SE-40/LE-37)-F1#2-065	17.9	4.1	3.0	0.6	16	11	55.4	95	206	5	763	763
51	(SE-40/LE-37)-F1#2-066	20.7	3.8	2.7	0.6	14	10	52.0	92	215	10	743	763
52	(SE-40/LE-37)-F1#2-067	21.9	3.5	2.3	0.6	12	12	45.2	68	210	4	787	–
53	(SE-40/LE-37)-F1#2-069	19.6	3.9	2.6	0.7	18	13	45.7	91	218	5	763	–
54	(SE-40/LE-37)-F1#2-070	19.7	4.0	2.8	0.6	20	12	44.9	100	224	10	743	763
55	(SE-40/LE-37)-F1#2-071	21.2	3.4	2.3	0.6	14	12	44.5	91	209	10	743	763
56	(SE-40/LE-37)-F1#2-072	18.6	3.3	2.4	0.5	12	12	41.2	57	211	5	787	800
57	(SE-40/LE-37)-F1#2-073	22.2	3.8	2.5	0.7	18	11	42.0	101	224	12	800	813
58	(SE-40/LE-37)-F1#2-074	16.7	4.4	3.1	0.7	18	10	71.8	70	186	13	743	763
59	(SE-40/LE-37)-F1#2-077	19.8	4.6	3.4	0.6	20	11	48.2	106	206	10	763	–
60	(SE-40/LE-37)-F1#2-078	21.2	4.3	2.9	0.7	18	11	58.0	123	208	6	763	763
61	(SE-40/LE-37)-F1#2-079	11.1	3.7	2.5	0.6	16	13	34.6	32	170	9	763	–
62	(SE-40/LE-37)-F1#2-080	15.7	3.9	2.7	0.6	18	14	39.8	77	200	7	763	763
63	(SE-40/LE-37)-F1#2-082	22.3	3.9	2.9	0.5	16	10	52.4	97	208	5	763	800
64	(SE-40/LE-37)-F1#2-083	12.5	4.5	3.1	0.7	22	10	54.6	69	220	11	775	800
65	(SE-40/LE-37)-F1#2-084	20.8	4.1	2.8	0.7	18	11	58.3	106	221	9	763	763
66	(SE-40/LE-37)-F1#2-085	15.5	4.2	2.8	0.7	18	11	50.4	70	216	13	743	–
67	(SE-40/LE-37)-F1#2-086	22.6	4.1	2.9	0.6	16	11	58.3	114	214	10	775	763
68	(SE-40/LE-37)-F1#2-087	21.2	4.1	2.8	0.7	14	12	47.7	118	223	3	763	763
69	(SE-40/LE-37)-F1#2-088	18.8	4.2	2.8	0.7	20	11	49.6	94	211	13	763	–
70	(SE-40/LE-37)-F1#2-089	21.0	3.9	2.5	0.7	16	11	59.7	111	207	7	800	813

Table B1. (cont.)

Entry No.	Pedigree	EL	ED	CD	KD	KRN	K/5CM	KWT	GY	PLTHT	TB	Pgdd	Sgdd
		cm				no.		g/300k	g plt^{-1}	cm	no.	gdd	
71	(SE-40/LE-37)-F1#2-092	21.6	4.5	3.1	0.7	16	11	59.3	123	209	10	775	–
72	(SE-40/LE-37)-F1#2-093	18.0	4.1	2.9	0.6	16	14	56.3	108	199	10	752	763
73	(SE-40/LE-37)-F1#2-094	20.7	4.6	2.8	0.9	20	10	54.1	120	216	13	743	743
74	(SE-40/LE-37)-F1#2-096	18.6	4.5	2.7	0.9	20	12	62.2	126	204	9	752	763
75	(SE-40/LE-37)-F1#2-097	19.2	3.9	2.5	0.7	16	12	62.4	100	235	7	787	–
76	(SE-40/LE-37)-F1#2-098	15.9	3.9	2.6	0.7	18	14	46.4	84	197	8	787	–
77	(SE-40/LE-37)-F1#2-099	18.6	3.4	2.2	0.6	12	12	56.2	79	232	2	800	800
78	(SE-40/LE-37)-F1#2-100	19.3	3.9	2.7	0.6	20	12	44.9	99	192	12	787	800
79	(SE-40/LE-37)-F1#2-101	20.0	4.1	2.9	0.6	18	12	49.1	106	235	12	752	752
80	(SE-40/LE-37)-F1#2-104	21.9	4.1	2.8	0.7	16	10	53.9	116	213	8	787	813
81	(SE-40/LE-37)-F1#2-107	16.8	3.7	2.7	0.5	18	11	49.7	79	208	10	763	787
82	(SE-40/LE-37)-F1#2-108	23.2	3.9	2.8	0.6	16	10	54.5	107	216	5	800	787
83	(SE-40/LE-37)-F1#2-109	19.9	3.7	2.4	0.7	16	13	42.7	89	216	7	787	800
84	(SE-40/LE-37)-F1#2-111	17.0	4.1	2.9	0.6	20	10	52.4	70	224	9	775	–
85	(SE-40/LE-37)-F1#2-112	19.7	4.5	3.0	0.8	20	12	46.1	105	220	10	763	–
86	(SE-40/LE-37)-F1#2-113	19.1	4.0	2.5	0.8	18	12	42.6	108	203	15	743	743
87	(SE-40/LE-37)-F1#2-114	20.0	3.9	2.6	0.7	18	12	47.4	102	215	14	752	752
88	(SE-40/LE-37)-F1#2-116	21.9	3.9	2.7	0.6	16	12	54.6	106	216	4	763	763
89	(SE-40/LE-37)-F1#2-118	21.2	4.3	2.9	0.7	18	13	60.7	122	208	11	752	752
90	(SE-40/LE-37)-F1#2-122	20.0	4.0	2.6	0.7	14	12	56.5	92	200	5	763	763
91	(SE-40/LE-37)-F1#2-125	18.9	4.1	2.9	0.6	16	11	62.4	124	222	4	775	787
92	(SE-40/LE-37)-F1#2-126	22.2	4.2	2.8	0.7	16	12	58.9	119	197	12	743	743
93	(SE-40/LE-37)-F1#2-127	21.7	3.7	2.4	0.7	16	12	46.7	88	199	15	763	775
94	(SE-40/LE-37)-F1#2-128	18.7	4.1	3.0	0.6	20	12	42.8	88	225	13	763	–
95	(SE-40/LE-37)-F1#2-129	18.2	3.9	2.6	0.7	16	13	43.0	82	221	7	787	813
96	(SE-40/LE-37)-F1#2-130	15.3	3.9	2.4	0.8	18	14	34.7	60	202	11	813	848
97	(SE-40/LE-37)-F1#2-131	14.2	4.2	2.5	0.9	20	13	42.9	78	207	13	787	–
98	(SE-40/LE-37)-F1#2-132	18.8	4.1	2.8	0.7	18	13	44.5	86	223	9	787	–
99	(SE-40/LE-37)-F1#2-134	18.8	4.0	2.7	0.7	16	12	68.2	125	198	8	743	743
100	(SE-40/LE-37)-F1#2-139	16.7	4.3	2.7	0.8	16	13	67.0	110	213	9	787	787
101	(SE-40/LE-37)-F1#2-140	19.0	3.9	2.8	0.6	14	11	49.8	68	207	11	787	800
102	(SE-40/LE-37)-F1#2-141	20.8	4.4	3.2	0.6	18	12	59.3	128	216	13	763	775
103	(SE-40/LE-37)-F1#2-142	18.8	4.1	2.9	0.6	16	12	45.6	74	211	3	763	775
104	(SE-40/LE-37)-F1#2-143	17.2	4.5	2.7	0.9	22	12	49.6	88	182	16	734	734
105	(SE-40/LE-37)-F1#2-144	19.5	3.7	2.5	0.6	16	9	52.1	61	230	9	800	–
106	(SE-40/LE-37)-F1#2-145	19.7	3.6	2.2	0.7	16	12	44.8	87	205	8	800	–
107	(SE-40/LE-37)-F1#2-146	13.4	4.4	2.8	0.8	16	12	61.1	78	204	6	743	743
108	(SE-40/LE-37)-F1#2-148	20.1	4.3	2.7	0.8	16	13	57.9	126	211	8	763	763
109	(SE-40/LE-37)-F1#2-149	21.5	4.0	2.7	0.7	18	13	44.7	93	203	10	800	800
110	(SE-40/LE-37)-F1#2-152	16.1	4.1	2.6	0.8	16	13	50.7	66	192	10	763	–

Table B1. (cont.)

Entry No.	Pedigree	EL	ED	CD	KD	KRN	K/SCM	KWT	GY	PLTHT	TB	Pgdd	Sgdd
		cm				no.		g/300k	g plt^{-1}	cm	no.	gdd	
111	(SE-40/LE-37)-F1#2-153	19.6	4.1	2.8	0.7	16	11	49.0	93	220	7	775	775
112	(SE-40/LE-37)-F1#2-154	20.2	4.0	2.6	0.7	18	12	52.1	107	225	9	763	787
113	(SE-40/LE-37)-F1#2-155	19.5	4.6	3.0	0.8	20	11	61.1	131	230	9	752	775
114	(SE-40/LE-37)-F1#2-156	21.6	4.4	2.9	0.8	20	12	48.2	115	224	3	775	775
115	(SE-40/LE-37)-F1#2-157	17.6	4.0	2.8	0.6	16	11	45.7	78	212	8	763	787
116	(SE-40/LE-37)-F1#2-158	20.3	4.1	2.8	0.7	16	13	58.2	118	226	8	752	763
117	(SE-40/LE-37)-F1#2-159	15.2	3.8	2.7	0.6	14	15	37.8	41	200	11	800	813
118	(SE-40/LE-37)-F1#2-161	20.4	4.4	3.1	0.7	18	12	57.5	103	212	10	752	775
119	(SE-40/LE-37)-F1#2-162	18.7	4.7	3.1	0.8	18	11	70.6	127	206	4	763	787
120	(SE-40/LE-37)-F1#2-163	14.5	3.4	2.2	0.6	16	11	36.6	46	208	4	848	875
121	(SE-40/LE-37)-F1#2-164	18.6	4.1	2.8	0.7	16	13	44.2	76	215	9	787	–
122	(SE-40/LE-37)-F1#2-167	20.2	3.9	2.8	0.6	14	11	65.2	116	192	11	743	743
123	(SE-40/LE-37)-F1#2-168	16.4	4.4	3.1	0.7	20	12	49.4	88	200	11	734	734
124	(SE-40/LE-37)-F1#2-169	20.2	3.9	2.7	0.6	14	11	61.1	94	221	4	800	–
125	(SE-40/LE-37)-F1#2-170	22.9	3.7	2.6	0.6	16	12	42.1	95	235	7	763	–
126	(SE-40/LE-37)-F1#2-171	15.2	4.0	2.6	0.7	16	12	46.0	51	200	9	800	–
127	(SE-40/LE-37)-F1#2-172	18.7	4.6	3.0	0.8	20	12	51.3	106	209	13	743	752
128	(SE-40/LE-37)-F1#2-173	19.8	4.1	2.6	0.8	16	12	54.6	104	215	12	763	787
129	(SE-40/LE-37)-F1#2-174	19.0	3.9	2.4	0.8	16	13	43.4	100	205	5	800	800
130	(SE-40/LE-37)-F1#2-176	21.2	4.5	2.9	0.8	20	12	60.6	128	220	9	752	787
131	(SE-40/LE-37)-F1#2-177	18.9	3.7	2.6	0.6	18	13	42.9	88	202	8	763	763
132	(SE-40/LE-37)-F1#2-178	23.7	4.0	2.7	0.7	18	10	48.0	110	215	10	752	763
133	(SE-40/LE-37)-F1#2-179	22.4	4.2	2.8	0.7	16	11	66.4	133	230	6	752	775
134	(SE-40/LE-37)-F1#2-182	18.7	4.1	2.7	0.7	16	13	46.6	87	220	–	752	752
135	(SE-40/LE-37)-F1#2-183	18.0	4.2	2.8	0.7	20	12	41.9	100	230	4	763	775
136	(SE-40/LE-37)-F1#2-184	19.0	4.1	2.4	0.9	16	13	55.9	119	227	4	775	775
137	(SE-40/LE-37)-F1#2-185	19.6	3.9	2.4	0.8	16	12	57.4	110	203	7	800	813
138	(SE-40/LE-37)-F1#2-187	17.3	4.2	2.9	0.7	20	11	51.1	110	216	16	800	800
139	(SE-40/LE-37)-F1#2-188	19.3	4.2	2.8	0.7	14	13	68.9	133	231	6	763	787
140	(SE-40/LE-37)-F1#2-189	20.1	4.2	2.7	0.8	18	11	66.5	120	212	13	743	763
141	(SE-40/LE-37)-F1#2-190	15.0	3.9	2.8	0.6	16	14	36.8	55	200	8	800	848
142	(SE-40/LE-37)-F1#2-191	19.8	4.1	2.6	0.8	14	12	59.5	113	202	11	763	800
143	(SE-40/LE-37)-F1#2-192	12.5	4.3	2.9	0.7	16	10	65.6	89	190	11	763	775
144	(SE-40/LE-37)-F1#2-193	19.6	3.8	2.3	0.8	14	15	60.5	111	213	5	775	787
145	(SE-40/LE-37)-F1#2-194	22.5	4.2	2.7	0.8	16	9	99.1	144	205	8	763	775
146	(SE-40/LE-37)-F1#2-197	20.6	3.5	2.2	0.7	14	13	48.5	127	226	6	752	763
147	(SE-40/LE-37)-F1#2-198	16.2	3.9	2.3	0.8	18	13	41.2	62	177	15	800	–
148	(SE-40/LE-37)-F1#2-199	16.8	4.3	2.8	0.8	20	11	49.6	74	205	8	763	787
149	(SE-40/LE-37)-F1#2-200	19.0	4.1	2.8	0.7	18	14	48.9	107	202	12	743	743
150	(SE-40/LE-37)-F1#2-201	18.7	3.6	2.5	0.6	18	12	36.2	86	216	10	752	–

Table B1. (cont.)

Entry No.	Pedigree	EL	ED	CD	KD	KRN	K/5CM	KWT	GY	PLTHT	TB	Pgdd	Sgdd
		cm				no.		g/300k	g plt^{-1}	cm	no.	gdd	
151	(SE-40/LE-37)-F1#2-202	20.7	4.1	2.6	0.8	14	12	61.7	111	202	7	800	800
152	(SE-40/LE-37)-F1#2-203	16.3	3.8	2.3	0.8	18	13	39.0	62	205	8	800	823
153	(SE-40/LE-37)-F1#2-204	15.8	4.1	2.3	0.9	18	11	58.0	73	185	11	752	763
154	(SE-40/LE-37)-F1#2-205	20.0	4.0	2.7	0.7	14	13	64.5	118	232	6	743	743
155	(SE-40/LE-37)-F1#2-206	19.5	4.4	2.8	0.8	18	13	53.4	117	215	11	775	775
156	(SE-40/LE-37)-F1#2-208	20.2	4.1	3.1	0.5	18	11	57.5	114	202	13	763	787
157	(SE-40/LE-37)-F1#2-212	17.6	3.9	2.7	0.6	16	14	49.7	101	190	10	775	813
158	(SE-40/LE-37)-F1#2-213	13.5	4.2	2.8	0.7	20	13	43.4	75	201	12	763	–
159	(SE-40/LE-37)-F1#2-214	17.8	3.5	2.3	0.6	16	13	42.3	70	203	10	848	862
160	(SE-40/LE-37)-F1#2-216	17.1	3.9	2.5	0.7	16	13	44.0	75	231	7	800	–
161	(SE-40/LE-37)-F1#2-217	20.6	3.9	2.6	0.7	16	10	59.0	99	216	7	763	–
162	(SE-40/LE-37)-F1#2-218	18.3	4.3	2.8	0.8	22	12	57.9	135	222	7	763	800
163	(SE-40/LE-37)-F1#2-219	15.4	4.1	2.9	0.6	20	13	36.9	73	212	5	775	–
164	(SE-40/LE-37)-F1#2-220	19.2	4.1	2.6	0.8	16	13	47.9	97	214	7	813	813
165	(SE-40/LE-37)-F1#2-221	17.7	4.1	2.8	0.7	18	12	45.2	106	198	10	763	763
166	(SE-40/LE-37)-F1#2-222	20.1	4.4	3.1	0.7	20	11	49.4	110	217	7	775	–
167	(SE-40/LE-37)-F1#2-224	18.8	3.7	2.5	0.6	14	11	53.3	90	217	8	775	775
168	(SE-40/LE-37)-F1#2-227	22.4	4.0	2.8	0.6	16	11	56.1	106	206	3	763	775
169	(SE-40/LE-37)-F1#2-229	21.7	3.8	2.4	0.7	16	17	41.1	108	194	11	763	763
170	(SE-40/LE-37)-F1#2-230	18.7	3.9	2.7	0.6	14	11	60.5	99	227	3	775	775
171	(SE-40/LE-37)-F1#2-231	19.2	3.9	2.8	0.6	16	10	57.1	84	217	5	775	–
172	(SE-40/LE-37)-F1#2-232	23.9	3.8	2.5	0.7	14	12	62.7	134	235	7	787	813
173	(SE-40/LE-37)-F1#2-233	22.5	3.8	2.7	0.6	16	13	41.6	108	208	6	800	800
174	(SE-40/LE-37)-F1#2-234	18.1	3.8	2.5	0.7	14	14	49.8	83	208	11	787	800
175	(SE-40/LE-37)-F1#2-235	20.1	4.0	2.7	0.7	14	14	57.0	124	221	2	775	775
176	(SE-40/LE-37)-F1#2-236	15.0	4.0	2.4	0.8	16	14	47.1	55	173	10	800	813
177	(SE-40/LE-37)-F1#2-237	19.4	4.4	2.9	0.8	20	13	44.7	113	215	9	763	775
178	(SE-40/LE-37)-F1#2-238	21.8	3.5	2.4	0.6	14	12	42.3	86	212	7	787	813
179	(SE-40/LE-37)-F1#2-242	21.6	3.4	2.5	0.5	12	12	52.1	103	213	5	775	775
180	(SE-40/LE-37)-F1#2-243	19.4	3.8	2.8	0.5	18	12	46.1	92	208	4	775	787
181	(SE-40/LE-37)-F1#2-244	22.1	3.9	2.7	0.6	16	13	48.6	114	223	11	763	775
182	(SE-40/LE-37)-F1#2-245	14.3	4.1	2.7	0.7	20	12	41.6	68	205	16	800	–
183	(SE-40/LE-37)-F1#2-246	17.2	4.1	2.9	0.6	14	13	63.3	111	205	4	763	775
184	(SE-40/LE-37)-F1#2-247	17.2	3.7	2.8	0.5	16	14	49.4	91	224	7	743	787
185	(SE-40/LE-37)-F1#2-248	15.2	4.3	2.5	0.9	20	13	50.0	85	207	10	743	752
186	(SE-40/LE-37)-F1#2-251	Discarded from analysis											
187	(SE-40/LE-37)-F1#2-252	20.0	4.1	2.6	0.8	16	13	58.1	122	242	10	734	734
188	(SE-40/LE-37)-F1#2-253	15.6	4.1	2.9	0.6	16	13	54.3	104	236	7	743	775
189	(SE-40/LE-37)-F1#2-254	16.7	4.3	2.8	0.8	18	12	52.0	108	218	14	743	743

APPENDIX C
MEANS, VARIANCES, AND HERITABILITIES FROM INDIVIDUAL PLANTS

Table C1. Means, variances, and four estimates of broad-sense heritability (h^2) for 10 traits measured on individual plants of the parents and generations of the SE-40×LE-37 maize population grown near Ames, IA in 2000.

		Parent or Generation											h^2 †			
		SE-40			LE-37			F_1			F_2					
Trait ‡	units	n §	$\bar{x}$	S^2	n	$\bar{x}$	S^2	n	$\bar{x}$	S^2	n	$\bar{x}$	S^2	Burton	M & K	W & M	Mod. W & M
EL	cm	120	8.3	2.4	120	22.5	3.4	117	22.1	1.2	188	18.8	6.1	0.80	0.53	0.65	0.65
ED	cm	109	4.1	0.0	20	3.2	0.0	117	4.6	0.0	188	4.0	0.1	0.59	0.76	0.71	0.11
CD	cm	109	2.7	0.0	20	2.3	0.0	117	3.0	0.0	188	2.7	0.1	0.64	0.66	0.65	–0.14
KD	cm	109	0.7	0.0	2	0.4	0.0	117	0.8	0.0	188	0.7	0.0	0.21	0.64	0.53	–1.19
KRN	no.	120	18	3	119	13	1	117	18	2	188	17	4	0.49	0.62	0.58	0.57
K/5CM	no.	104	12	2	8	9	1	117	12	0	188	12	1	0.68	0.35	0.48	0.34
KWT	g	46	50.1	100.0	18	71.3	152.9	117	66.3	49.1	188	52	92	0.47	–0.34	0.01	0.62
GY	g plant^{-1}	48	48	74	6	53	266	117	176	749	188	93	525	–0.43	0.73	0.53	0.86
PLTHT	cm	118	170	46	119	186	233	117	239	107	188	210	170	0.37	0.39	0.38	0.77
TB	no.	119	11	4	119	2	1	117	11	8	186	9	12	0.30	0.81	0.70	0.74

† Formulas for each h^2 estimation can be found in appendix A and are labeled for those researchers whom proposed the formulas. Burton = Burton (1951); M & K = Mahmud and Kramer (1951); W & M = Weber and Moorthy (1952); Mod. W & M = Modified Weber and Moorthy.

‡ EL = ear length, ED = ear diameter, CD = cob diameter, KD = kernel depth, KRN = kernel-row number, K/5CM = kernels per 5 cm of EL, KWT = weight of 300 kernels, GY = grain yield, PLTHT = plant height, and TB = number of secondary tassel branches.

§ n = number of plants represented in the mean ($\bar{x}$) and variance (S^2)

APPENDIX D

ANALYSES OF VARIANCE FOR $F_{2:3}$ DATA COMBINED ACROSS FOUR ENVIRONMENTS

Table D1. Analysis of variance of 10 traits, evaluated on 188 $F_{2:3}$ progeny from the SE-40×LE-37 maize population, and combined across four Iowa environments in 2001.

Sources of variation	Ear length		Ear diameter		Cob diameter		Kernel depth		Kernel-row number	
	df	Mean squares	df	Mean squares	df	Mean squares	df	Mean squares	df	Mean squares
Environments (E)	3	101.0 **	3	0.74 **	3	0.27 **	3	0.233 **	3	22.0 **
Genotypes (G)	198	17.2 **	198	0.35 **	198	0.13 **	198	0.030 **	198	6.7 **
$F_{2:3}$ progeny (F)	187	8.5 **	187	0.16 **	187	0.08 **	187	0.020 **	187	4.6 **
Checks (CH)	10	176.9 **	10	3.73 **	10	1.03 **	10	0.228 **	10	44.1 **
F vs. CH	1	52.7 **	1	1.41	1	1.08	1	0.006	1	33.7 **
E X G	594	0.6	594	0.06 **	594	0.04 **	594	0.004	594	0.6
E X F	561	0.5	561	0.03 **	561	0.02 **	561	0.002	561	0.3
E X CH	30	0.8	30	0.66 **	30	0.35 **	30	0.025 **	30	5.7 **
E X (F vs. CH)	3	2.1 *	3	0.80 **	3	0.42 **	3	0.020 **	3	0.9
Pooled Error	559	0.8	549	0.01	549	0.01	549	0.004	549	0.6
Heritability (h^2) †	0.94		0.81		0.75		0.90		0.94	
95% CI of h^2 ‡	0.93–0.95		0.77–0.85		0.69–0.80		0.88–0.92		0.92–0.95	

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.
† h^2 on a progeny-mean basis.
‡ 95%-confidence interval for h^2.

Table D1. (cont.)

Sources of variation	Kernels / 5 cm		Kernel weight		Grain yield		Plant height		Tassel-branch number	
	df	Mean squares	df	Mean squares	df	Mean squares	df	Mean squares	df	Mean squares
Environments (E)	3	282.5 **	3	5482 **	3	22576 **	3	2584 **	3	77.1 **
Genotypes (G)	198	3.8 **	198	233 **	198	2662 **	198	406 **	198	17.8 **
$F_{2:3}$ progeny (F)	187	2.9 **	187	191 **	187	995 **	187	340 **	187	16.6 **
Checks (CH)	10	14.8 **	10	1038 **	10	33413 **	10	1540 **	10	40.3 **
F vs. CH	1	52.7 *	1	17	1	6920 **	1	1407 *	1	0.1
E X G	594	0.7	594	67 **	594	145	594	28	594	0.7
E X F	561	0.5	561	46 **	561	132	561	28	561	0.7
E X CH	30	3.5 **	30	382 **	30	392 **	30	26	30	1.1
E X (F vs. CH)	3	2.2 *	3	791 **	3	157	3	68	3	2.4 *
Pooled Error	548	0.7	528	26	548	216	567	33	568	0.9
Heritability	0.83		0.76		0.87		0.92		0.96	
95% CI of h^2	0.78–0.86		0.70–0.81		0.83–0.90		0.90–0.94		0.95–0.97	

APPENDIX E

PHENOTYPE MEANS ACROSS FOUR ENVIRONMENTS IN 2001

Table E1. Mean performance of all entries from experiment 19 ($F_{2:3}$ progeny of the SE-40×LE-37 maize population) grown near Ames, Ankeny, Crawfordsville, and Lewis IA, in 2001.

Entry No. †	Pedigree	EL‡	ED	CD	KD	KRN	K/5CM§	KWT¶	GY	PLTHT#	TB††	Pgdd‡‡	Sgdd
		cm				no.		g/300k	g plt^{-1}	cm	no.	gdd	
1	(SE-40/LE-37)-F1#2-002	17.5	3.7	2.5	0.6	13	11	67.3	96	156	5	875	902
2	(SE-40/LE-37)-F1#2-003	18.5	3.9	2.7	0.6	15	11	63.1	90	155	8	875	921
3	(SE-40/LE-37)-F1#2-004	14.7	3.7	2.4	0.6	14	12	65.7	89	149	7	883	908
4	(SE-40/LE-37)-F1#2-005	17.4	3.7	2.7	0.5	15	12	55.5	93	156	9	881	920
5	(SE-40/LE-37)-F1#2-006	17.8	3.7	2.9	0.4	13	9	75.9	43	157	9	921	1024
6	(SE-40/LE-37)-F1#2-007	15.7	3.9	2.7	0.6	15	11	75.6	79	147	6	884	961
7	(SE-40/LE-37)-F1#2-008	17.8	3.9	2.7	0.6	15	12	57.4	103	139	6	867	887
8	(SE-40/LE-37)-F1#2-009	18.3	3.8	2.6	0.6	14	11	68.4	97	156	10	866	896
9	(SE-40/LE-37)-F1#2-010	19.3	4.1	2.9	0.6	14	10	77.2	101	161	9	875	904
10	(SE-40/LE-37)-F1#2-012	16.2	3.9	2.6	0.7	15	11	66.6	98	153	5	868	867
11	(SE-40/LE-37)-F1#2-013	15.7	4.1	2.9	0.6	16	11	65.0	74	146	10	884	953
12	(SE-40/LE-37)-F1#2-014	17.8	3.8	2.7	0.5	14	11	65.9	73	161	7	897	943
13	(SE-40/LE-37)-F1#2-017	17.0	4.1	2.6	0.7	15	12	71.3	102	147	7	876	929
14	(SE-40/LE-37)-F1#2-018	14.7	3.8	2.7	0.6	15	12	48.1	57	148	11	915	976
15	(SE-40/LE-37)-F1#2-019	19.6	3.7	2.7	0.5	13	7	73.4	59	167	12	897	983
16	(SE-40/LE-37)-F1#2-020	17.3	3.7	2.6	0.6	14	12	59.2	81	164	11	889	969
17	(SE-40/LE-37)-F1#2-021	16.4	3.7	2.5	0.6	14	12	60.6	92	154	6	827	866
18	(SE-40/LE-37)-F1#2-022	18.5	3.7	2.5	0.6	14	12	61.8	91	185	9	883	921
19	(SE-40/LE-37)-F1#2-023	17.8	3.9	2.6	0.6	15	12	59.2	91	159	9	867	915
20	(SE-40/LE-37)-F1#2-025	15.8	3.9	2.6	0.7	14	12	70.1	107	159	9	858	882
21	(SE-40/LE-37)-F1#2-026	18.6	3.8	2.9	0.4	13	10	82.5	62	177	10	916	963
22	(SE-40/LE-37)-F1#2-027	15.5	3.9	2.5	0.7	15	11	72.3	82	152	7	873	912
23	(SE-40/LE-37)-F1#2-028	16.7	4.0	2.7	0.6	15	11	71.5	99	163	9	878	916
24	(SE-40/LE-37)-F1#2-029	18.0	3.5	2.7	0.4	12	9	75.0	55	159	10	915	955
25	(SE-40/LE-37)-F1#2-032	18.9	3.7	2.4	0.7	14	11	69.1	106	171	7	897	936
26	(SE-40/LE-37)-F1#2-034	14.9	3.9	2.6	0.7	16	11	65.6	92	168	9	859	896
27	(SE-40/LE-37)-F1#2-036	16.0	3.9	2.6	0.7	15	11	69.2	85	156	9	881	921
28	(SE-40/LE-37)-F1#2-037	14.6	4.1	2.8	0.7	15	10	75.4	86	156	8	898	937
29	(SE-40/LE-37)-F1#2-038	17.5	3.9	2.5	0.7	15	12	62.8	114	160	8	852	890
30	(SE-40/LE-37)-F1#2-039	16.4	3.8	2.5	0.6	15	12	64.5	97	137	4	875	914

† Entry number of a genotype in experiment 19 evaluated in 2001.

‡ EL (ear length), ED (ear diameter), CD (cob diameter), KD (kernel depth), and KRN (kernel-row number) data were obtained from measurements on the primary ear from 10 plants per plot.

§ K/5CM (kernels per 5 cm) data were obtained from measurements on the primary ear from five plants per plot.

¶ KWT (kernel weight) was obtained by weighing 300 kernels, and GY (grain yield) by weighing all kernels from all seed-bearing ears harvested from 10 plants per plot.

PLTHT (plant height) was measured from the soil surface to the terminal node on 10 plants per plot.

†† TB (number of secondary tassel branches) was obtained from 10 plant per plot.

‡‡ Pgdd and Sgdd = growing degree days (°C) when 50% of the plants showed male or female anthesis, respectively. Pgdd and Sgdd were measured at the Ames, IA, 2001 environment only.

Table E1. (cont.)

Entry No.	Pedigree	EL	ED	CD	KD	KRN	K/5CM	KWT	GY	PLTHT	TB	Pgdd	Sgdd
		cm				no.		g/300k	g plt^{-1}	cm	no.	gdd	
31	(SE-40/LE-37)-F1#2-040	12.9	4.0	2.8	0.6	14	12	68.7	80	138	4	882	917
32	(SE-40/LE-37)-F1#2-041	17.8	3.9	2.6	0.6	16	11	59.2	105	164	5	843	881
33	(SE-40/LE-37)-F1#2-043	17.2	4.1	2.8	0.7	16	11	60.8	90	154	12	868	910
34	(SE-40/LE-37)-F1#2-044	17.9	4.0	2.8	0.6	15	10	78.5	91	172	9	889	946
35	(SE-40/LE-37)-F1#2-047	15.4	3.8	2.8	0.5	15	11	61.4	76	147	7	883	896
36	(SE-40/LE-37)-F1#2-049	16.6	4.3	2.9	0.7	16	10	80.7	112	154	5	866	881
37	(SE-40/LE-37)-F1#2-050	17.9	4.2	2.7	0.7	15	11	76.1	125	157	8	840	849
38	(SE-40/LE-37)-F1#2-051	16.6	3.9	2.5	0.7	15	10	77.5	108	166	6	875	882
39	(SE-40/LE-37)-F1#2-052	16.9	3.8	2.5	0.7	15	12	60.2	106	149	10	866	866
40	(SE-40/LE-37)-F1#2-053	16.4	2.7	2.1	0.3	13	7	58.9	32	174	9	993	1056
41	(SE-40/LE-37)-F1#2-054	18.2	3.9	2.7	0.6	14	11	66.9	89	164	12	903	928
42	(SE-40/LE-37)-F1#2-055	13.4	3.9	2.6	0.7	14	10	80.0	90	158	5	858	881
43	(SE-40/LE-37)-F1#2-056	18.1	3.8	2.6	0.6	14	11	64.0	100	157	5	874	928
44	(SE-40/LE-37)-F1#2-057	17.4	4.0	2.7	0.6	15	12	57.2	100	167	10	866	909
45	(SE-40/LE-37)-F1#2-058	17.5	4.1	2.9	0.6	14	10	89.9	92	175	7	883	951
46	(SE-40/LE-37)-F1#2-059	18.2	4.0	2.7	0.6	15	10	65.9	81	151	10	904	963
47	(SE-40/LE-37)-F1#2-062	17.4	3.9	2.6	0.7	17	12	57.3	104	150	7	849	916
48	(SE-40/LE-37)-F1#2-063	16.8	3.7	2.6	0.6	14	11	74.1	81	176	11	910	942
49	(SE-40/LE-37)-F1#2-064	18.5	3.7	2.7	0.5	15	10	65.6	77	152	10	874	900
50	(SE-40/LE-37)-F1#2-065	16.2	4.1	2.8	0.6	15	11	78.5	104	155	4	851	867
51	(SE-40/LE-37)-F1#2-066	16.1	3.9	2.6	0.6	14	10	75.3	95	163	8	834	868
52	(SE-40/LE-37)-F1#2-067	17.6	3.6	2.5	0.6	13	10	78.8	64	164	8	896	954
53	(SE-40/LE-37)-F1#2-069	18.3	4.1	2.8	0.7	15	11	76.8	104	165	7	874	954
54	(SE-40/LE-37)-F1#2-070	17.0	3.9	2.7	0.6	15	11	66.6	98	164	5	859	909
55	(SE-40/LE-37)-F1#2-071	17.3	3.9	2.5	0.7	14	11	68.0	115	155	7	875	882
56	(SE-40/LE-37)-F1#2-072	18.6	3.4	2.4	0.5	12	11	60.7	77	165	6	880	926
57	(SE-40/LE-37)-F1#2-073	18.4	3.9	2.6	0.6	15	10	76.2	106	175	9	904	954
58	(SE-40/LE-37)-F1#2-074	15.6	4.2	2.8	0.7	16	10	51.9	96	150	9	859	904
59	(SE-40/LE-37)-F1#2-077	17.4	4.2	3.1	0.5	16	10	64.9	87	157	9	884	936
60	(SE-40/LE-37)-F1#2-078	17.6	3.8	2.6	0.6	15	12	66.1	100	146	4	841	882
61	(SE-40/LE-37)-F1#2-079	14.1	3.9	2.7	0.6	14	12	66.8	62	138	12	882	976
62	(SE-40/LE-37)-F1#2-080	17.2	4.1	2.7	0.7	16	12	67.0	108	161	9	883	933
63	(SE-40/LE-37)-F1#2-082	18.3	4.0	2.8	0.6	14	10	74.8	98	152	8	884	928
64	(SE-40/LE-37)-F1#2-083	16.3	4.2	2.9	0.7	16	11	75.1	93	167	8	873	927
65	(SE-40/LE-37)-F1#2-084	17.5	4.0	2.7	0.7	16	12	66.5	125	163	6	866	882
66	(SE-40/LE-37)-F1#2-085	14.7	4.1	2.8	0.7	15	11	75.4	83	161	9	867	953
67	(SE-40/LE-37)-F1#2-086	18.5	3.9	2.7	0.6	14	10	74.8	112	164	9	865	866
68	(SE-40/LE-37)-F1#2-087	17.3	3.7	2.5	0.6	13	11	68.9	87	162	11	882	921
69	(SE-40/LE-37)-F1#2-088	16.7	4.1	2.9	0.6	16	11	68.3	86	160	7	890	976
70	(SE-40/LE-37)-F1#2-089	18.9	3.8	2.6	0.6	14	10	77.3	95	165	7	902	955

Table E1. (cont.)

Entry No.	Pedigree	EL	ED	CD	KD	KRN	K/5CM	KWT	GY	PLTHT	TB	Pgdd	Sgdd
		cm				no.		g/300k	g plt^{-1}	cm	no.	gdd	
71	(SE-40/LE-37)-F1#2-092	17.8	4.0	2.8	0.6	14	10	80.6	91	163	10	910	983
72	(SE-40/LE-37)-F1#2-093	13.7	4.0	2.6	0.7	15	12	68.6	89	153	9	867	897
73	(SE-40/LE-37)-F1#2-094	16.4	4.3	2.8	0.7	18	12	68.2	110	166	8	875	922
74	(SE-40/LE-37)-F1#2-096	15.5	4.1	2.7	0.7	17	12	66.0	108	145	8	850	883
75	(SE-40/LE-37)-F1#2-097	17.4	3.9	2.6	0.6	15	11	72.2	101	167	7	874	934
76	(SE-40/LE-37)-F1#2-098	15.8	4.0	2.7	0.6	15	12	68.0	89	155	8	891	961
77	(SE-40/LE-37)-F1#2-099	15.7	3.6	2.5	0.6	13	10	77.7	77	168	4	897	910
78	(SE-40/LE-37)-F1#2-100	16.6	3.9	2.9	0.5	16	11	65.4	85	148	7	882	954
79	(SE-40/LE-37)-F1#2-101	15.7	4.0	2.8	0.6	16	11	55.7	97	174	9	882	903
80	(SE-40/LE-37)-F1#2-104	18.7	3.9	2.7	0.6	14	11	74.7	109	157	10	874	921
81	(SE-40/LE-37)-F1#2-107	18.6	4.1	2.7	0.7	15	11	78.3	120	165	6	876	910
82	(SE-40/LE-37)-F1#2-108	17.6	4.0	2.8	0.6	15	10	76.3	99	168	8	910	912
83	(SE-40/LE-37)-F1#2-109	18.8	3.8	2.5	0.6	14	11	72.0	104	161	6	865	899
84	(SE-40/LE-37)-F1#2-111	17.7	3.8	2.8	0.5	15	11	65.0	84	167	9	875	914
85	(SE-40/LE-37)-F1#2-112	17.6	4.2	2.9	0.7	17	11	66.3	97	171	10	890	962
86	(SE-40/LE-37)-F1#2-113	17.6	4.0	2.6	0.7	16	12	62.6	114	150	10	858	880
87	(SE-40/LE-37)-F1#2-114	17.8	3.9	2.6	0.7	15	11	69.0	118	158	10	867	867
88	(SE-40/LE-37)-F1#2-116	19.7	3.9	2.7	0.6	14	11	69.3	103	157	6	875	906
89	(SE-40/LE-37)-F1#2-118	17.9	3.8	2.6	0.6	14	12	68.1	108	163	8	867	898
90	(SE-40/LE-37)-F1#2-122	17.3	3.9	2.6	0.6	14	10	71.3	91	146	5	876	883
91	(SE-40/LE-37)-F1#2-125	14.0	3.9	2.8	0.6	15	10	72.8	74	173	7	883	933
92	(SE-40/LE-37)-F1#2-126	18.2	4.1	2.7	0.7	16	11	65.7	125	151	7	866	882
93	(SE-40/LE-37)-F1#2-127	18.8	3.9	2.7	0.6	15	11	63.4	105	155	8	858	910
94	(SE-40/LE-37)-F1#2-128	16.4	4.1	3.0	0.6	16	11	68.1	83	167	9	884	947
95	(SE-40/LE-37)-F1#2-129	17.6	3.9	2.8	0.5	14	10	70.6	66	164	8	890	957
96	(SE-40/LE-37)-F1#2-130	14.8	3.6	2.5	0.5	13	10	69.3	53	147	12	946	1009
97	(SE-40/LE-37)-F1#2-131	15.8	3.9	2.7	0.6	15	10	70.6	71	163	11	916	992
98	(SE-40/LE-37)-F1#2-132	18.2	3.9	2.8	0.5	14	11	66.2	81	165	11	883	953
99	(SE-40/LE-37)-F1#2-134	16.2	3.7	2.4	0.6	15	12	63.2	99	162	7	848	866
100	(SE-40/LE-37)-F1#2-139	14.2	4.0	2.5	0.7	15	13	73.1	93	160	8	883	908
101	(SE-40/LE-37)-F1#2-140	18.5	3.9	2.8	0.6	14	10	76.1	97	159	11	875	915
102	(SE-40/LE-37)-F1#2-141	17.0	4.2	2.8	0.7	16	11	64.7	109	168	10	866	868
103	(SE-40/LE-37)-F1#2-142	17.8	4.0	2.8	0.6	14	11	72.8	91	158	3	884	927
104	(SE-40/LE-37)-F1#2-143	18.4	4.2	2.7	0.7	16	11	67.9	99	144	9	867	910
105	(SE-40/LE-37)-F1#2-144	18.8	3.7	2.7	0.5	15	11	57.0	72	157	6	884	954
106	(SE-40/LE-37)-F1#2-145	17.5	3.8	2.7	0.6	14	10	69.1	77	168	8	915	953
107	(SE-40/LE-37)-F1#2-146	13.8	4.1	2.7	0.7	15	13	66.6	101	151	7	850	867
108	(SE-40/LE-37)-F1#2-148	16.0	3.9	2.7	0.6	14	12	69.0	95	167	10	891	921
109	(SE-40/LE-37)-F1#2-149	18.3	4.0	2.7	0.7	17	11	56.2	101	161	9	883	909
110	(SE-40/LE-37)-F1#2-152	17.3	4.0	2.7	0.6	15	12	60.9	89	143	11	849	909

Table E1. (cont.)

Entry No.	Pedigree	EL	ED	CD	KD	KRN	K/5CM	KWT	GY	PLTHT	TB	Pgdd	Sgdd
		--- cm ---				--- no. ---		g/300k	g plt^{-1}	cm	no.	--- gdd ---	
111	(SE-40/LE-37)-F1#2-153	18.3	3.9	2.7	0.6	14	11	71.2	109	166	7	874	893
112	(SE-40/LE-37)-F1#2-154	18.6	3.8	2.7	0.6	15	11	67.1	94	164	8	865	928
113	(SE-40/LE-37)-F1#2-155	16.9	4.1	2.9	0.6	17	11	68.9	108	172	8	887	946
114	(SE-40/LE-37)-F1#2-156	18.9	4.2	2.8	0.7	15	11	76.4	112	164	6	866	903
115	(SE-40/LE-37)-F1#2-157	16.4	3.8	2.7	0.6	14	11	67.7	87	159	8	883	922
116	(SE-40/LE-37)-F1#2-158	18.4	3.8	2.5	0.6	14	11	74.3	104	166	10	873	908
117	(SE-40/LE-37)-F1#2-159	16.2	3.9	2.7	0.6	14	11	65.1	64	162	11	898	941
118	(SE-40/LE-37)-F1#2-161	16.7	4.2	3.0	0.6	16	10	73.4	83	169	9	883	921
119	(SE-40/LE-37)-F1#2-162	18.0	4.0	2.8	0.6	14	11	80.7	85	156	5	882	907
120	(SE-40/LE-37)-F1#2-163	14.6	3.5	2.7	0.4	13	9	80.1	48	147	3	1032	1048
121	(SE-40/LE-37)-F1#2-164	18.1	3.9	2.8	0.6	14	11	68.1	76	169	8	904	962
122	(SE-40/LE-37)-F1#2-167	16.6	3.8	2.6	0.6	14	12	65.2	104	146	8	842	867
123	(SE-40/LE-37)-F1#2-168	15.9	4.1	2.9	0.6	16	12	65.5	106	155	5	832	865
124	(SE-40/LE-37)-F1#2-169	18.4	3.9	2.7	0.6	14	11	73.6	86	164	6	874	929
125	(SE-40/LE-37)-F1#2-170	19.6	3.8	2.6	0.6	15	11	64.9	108	167	7	857	903
126	(SE-40/LE-37)-F1#2-171	17.2	4.1	2.8	0.6	15	11	68.8	83	148	6	882	953
127	(SE-40/LE-37)-F1#2-172	17.4	4.2	3.0	0.6	17	11	61.8	91	151	11	867	934
128	(SE-40/LE-37)-F1#2-173	18.4	4.2	2.8	0.7	16	11	73.8	106	169	12	895	959
129	(SE-40/LE-37)-F1#2-174	16.8	3.8	2.5	0.7	14	12	67.9	91	146	5	910	928
130	(SE-40/LE-37)-F1#2-176	18.7	4.0	2.7	0.6	15	11	76.2	102	166	7	875	954
131	(SE-40/LE-37)-F1#2-177	18.7	3.7	2.6	0.5	14	12	57.3	90	149	8	867	904
132	(SE-40/LE-37)-F1#2-178	19.5	4.0	2.7	0.7	16	11	58.8	108	158	10	875	903
133	(SE-40/LE-37)-F1#2-179	19.5	3.8	2.6	0.6	15	11	69.0	103	169	7	853	889
134	(SE-40/LE-37)-F1#2-182	16.0	4.0	2.8	0.6	15	11	47.8	84	166	9	833	904
135	(SE-40/LE-37)-F1#2-183	16.6	4.0	2.6	0.7	16	12	59.5	102	168	5	867	896
136	(SE-40/LE-37)-F1#2-184	17.9	4.0	2.7	0.6	15	12	69.3	100	173	5	876	922
137	(SE-40/LE-37)-F1#2-185	13.8	3.9	2.7	0.6	15	11	74.1	81	157	7	927	954
138	(SE-40/LE-37)-F1#2-187	14.8	4.3	2.9	0.7	17	11	68.9	97	168	13	897	928
139	(SE-40/LE-37)-F1#2-188	15.9	3.9	2.5	0.7	15	11	75.2	94	164	7	883	914
140	(SE-40/LE-37)-F1#2-189	16.3	3.9	2.7	0.6	16	11	61.1	99	153	9	827	860
141	(SE-40/LE-37)-F1#2-190	16.2	4.1	3.0	0.6	17	12	54.2	85	159	9	874	920
142	(SE-40/LE-37)-F1#2-191	17.0	4.0	2.8	0.6	14	11	72.5	82	151	10	881	939
143	(SE-40/LE-37)-F1#2-192	13.5	4.3	2.8	0.7	15	12	75.9	95	149	7	850	889
144	(SE-40/LE-37)-F1#2-193	16.7	3.5	2.4	0.6	13	13	63.6	81	153	5	888	941
145	(SE-40/LE-37)-F1#2-194	17.7	3.9	2.5	0.7	16	11	67.1	106	153	7	858	867
146	(SE-40/LE-37)-F1#2-197	17.6	3.7	2.4	0.6	14	12	64.0	106	168	9	842	868
147	(SE-40/LE-37)-F1#2-198	16.4	3.6	2.5	0.6	14	11	64.7	53	133	10	916	979
148	(SE-40/LE-37)-F1#2-199	16.4	4.1	2.8	0.7	15	10	73.4	84	158	8	874	933
149	(SE-40/LE-37)-F1#2-200	16.7	3.8	2.5	0.6	15	12	58.9	91	146	8	857	880
150	(SE-40/LE-37)-F1#2-201	17.3	3.6	2.5	0.5	15	14	47.1	80	155	8	859	928

Table E1. (cont.)

Entry No.	Pedigree	EL	ED	CD	KD	KRN	K/5CM	KWT	GY	PLTHT	TB	Pgdd	Sgdd
		cm				no.		g/300k	g plt^{-1}	cm	no.	gdd	
151	(SE-40/LE-37)-F1#2-202	18.0	3.9	2.6	0.6	14	11	69.1	93	160	10	922	961
152	(SE-40/LE-37)-F1#2-203	16.3	3.7	2.7	0.5	14	11	58.1	71	170	6	909	975
153	(SE-40/LE-37)-F1#2-204	17.2	4.1	2.6	0.8	16	12	64.1	89	135	8	858	894
154	(SE-40/LE-37)-F1#2-205	17.6	3.8	2.5	0.7	14	11	64.9	98	169	8	845	883
155	(SE-40/LE-37)-F1#2-206	16.4	4.2	2.8	0.7	16	12	71.3	106	155	8	882	926
156	(SE-40/LE-37)-F1#2-208	19.1	4.1	2.8	0.6	15	10	71.5	107	155	8	882	922
157	(SE-40/LE-37)-F1#2-212	15.9	3.9	2.6	0.6	15	12	66.4	81	146	7	866	903
158	(SE-40/LE-37)-F1#2-213	14.3	4.0	2.7	0.7	15	12	66.2	83	145	9	841	887
159	(SE-40/LE-37)-F1#2-214	15.8	3.7	2.5	0.6	13	11	70.4	71	148	8	940	984
160	(SE-40/LE-37)-F1#2-216	16.1	3.7	2.6	0.6	14	11	73.7	76	171	9	874	940
161	(SE-40/LE-37)-F1#2-217	18.4	3.8	2.7	0.6	13	10	73.6	89	159	9	867	910
162	(SE-40/LE-37)-F1#2-218	15.1	4.2	2.8	0.7	18	11	72.3	105	166	6	895	933
163	(SE-40/LE-37)-F1#2-219	16.2	4.1	2.7	0.7	17	12	66.6	111	157	9	879	887
164	(SE-40/LE-37)-F1#2-220	17.7	3.6	2.5	0.6	13	10	72.3	80	163	9	935	992
165	(SE-40/LE-37)-F1#2-221	14.1	4.2	2.8	0.7	16	11	69.3	98	139	9	874	910
166	(SE-40/LE-37)-F1#2-222	17.3	3.8	2.8	0.5	14	9	75.3	57	159	8	904	968
167	(SE-40/LE-37)-F1#2-224	18.1	3.6	2.5	0.5	14	11	60.6	97	165	6	884	896
168	(SE-40/LE-37)-F1#2-227	17.7	3.9	2.8	0.5	15	10	71.9	81	152	7	881	926
169	(SE-40/LE-37)-F1#2-229	18.3	3.7	2.5	0.6	13	11	68.1	93	144	10	886	910
170	(SE-40/LE-37)-F1#2-230	16.3	4.0	2.7	0.6	14	11	82.8	96	157	4	867	889
171	(SE-40/LE-37)-F1#2-231	18.3	4.1	2.8	0.6	15	11	69.0	106	155	8	857	888
172	(SE-40/LE-37)-F1#2-232	19.8	3.7	2.4	0.6	13	11	79.6	116	177	9	883	910
173	(SE-40/LE-37)-F1#2-233	16.9	3.7	2.6	0.6	14	11	71.9	87	167	7	890	915
174	(SE-40/LE-37)-F1#2-234	16.7	4.0	2.7	0.7	14	12	70.3	93	161	8	882	909
175	(SE-40/LE-37)-F1#2-235	16.3	3.9	2.7	0.6	15	10	72.8	102	168	4	882	889
176	(SE-40/LE-37)-F1#2-236	13.9	4.0	2.8	0.6	15	11	66.1	84	153	14	922	953
177	(SE-40/LE-37)-F1#2-237	16.0	4.2	2.8	0.7	16	11	67.5	101	157	9	884	941
178	(SE-40/LE-37)-F1#2-238	17.9	3.7	2.4	0.6	14	12	65.8	107	158	7	897	916
179	(SE-40/LE-37)-F1#2-242	19.5	3.5	2.4	0.5	13	11	62.3	95	153	5	884	916
180	(SE-40/LE-37)-F1#2-243	18.4	3.8	2.7	0.5	15	11	60.9	95	147	6	882	914
181	(SE-40/LE-37)-F1#2-244	17.2	4.0	2.7	0.7	15	12	61.3	86	152	9	889	935
182	(SE-40/LE-37)-F1#2-245	16.0	3.8	2.6	0.6	15	11	72.0	72	160	14	903	984
183	(SE-40/LE-37)-F1#2-246	16.9	3.9	2.7	0.6	14	11	71.8	93	144	5	884	927
184	(SE-40/LE-37)-F1#2-247	14.5	4.0	2.6	0.7	16	12	63.3	82	159	6	876	929
185	(SE-40/LE-37)-F1#2-248	15.3	4.3	2.8	0.8	16	12	67.7	109	145	7	842	881
186	(SE-40/LE-37)-F1#2-251	Discarded from analysis											
187	(SE-40/LE-37)-F1#2-252	16.2	4.0	2.5	0.7	16	12	66.1	117	171	5	850	881
188	(SE-40/LE-37)-F1#2-253	14.3	3.9	2.7	0.6	15	12	64.5	84	158	8	875	916
189	(SE-40/LE-37)-F1#2-254	14.9	4.3	2.8	0.8	16	12	73.8	115	163	8	843	883

Table E1. (cont.)

Entry No.	Pedigree	EL	ED	CD	KD	KRN	K/5CM	KWT	GY	PLTHT	TB	Pgdd	Sgdd
		cm				no.		g/300k	g plt^{-1}	cm	no.	gdd	
190	LE-37	22.4	2.2	1.7	0.2	8	6	54.1	23	166	4	958	1025
191	LE-37	21.9	2.5	1.8	0.3	8	6	51.8	30	161	4	947	1003
192	LE-37	21.4	2.2	1.6	0.3	11	9	35.8	15	162	3	949	1027
193	SE-40	8.1	4.0	2.8	0.6	15	11	67.2	36	135	11	896	1017
194	SE-40	8.5	4.1	2.8	0.6	15	10	70.2	37	139	11	896	1010
195	SE-40	8.0	4.0	2.8	0.6	15	10	68.7	40	141	11	890	992
196	SE-40/LE-37	23.3	4.6	2.8	0.9	16	11	85.5	228	187	9	819	834
197	SE-40/LE-37	23.0	4.6	2.8	0.9	16	11	85.5	227	188	10	803	819
198	SE-40/LE-37	23.2	4.6	2.9	0.8	17	12	86.5	233	184	9	817	833
199	(SE-40/LE-37)/LE-37	23.0	3.8	2.7	0.6	14	11	75.9	148	180	6	884	903
200	(SE-40/LE-37)/SE-40	16.3	4.6	2.8	0.9	17	12	77.3	138	165	10	818	859
	EXPERIMENT MEAN	17.0	3.9	2.7	0.6	15	11	68.4	93	159	8	879	922
	MINIMUM MEAN	8.0	2.2	1.6	0.2	8	6	35.8	15	133	3	803	819
	MAXIMUM MEAN	23.3	4.6	3.1	0.9	18	14	89.9	233	188	14	1032	1056
	LSD(0.05) ‡‡	1.1	0.3	0.3	0.1	1	1	11.6	17	7	1	21	39
	F×E MS §§	0.5	0.03	0.02	0.002	0.3	0.5	46.2	132	28	0.7	108	378

‡‡ Least significant difference at 0.05 probability level. $LSD = 2\sqrt{\frac{2\,MS_{E\cdot G}}{4}}$; and may be used to compare means of all entries.

§§ F×E MS = the mean square for the $F_{2:3}$–progeny×environment interaction, which should be used to compute the LSD for comparison of $F_{2:3}$–progeny means only.

APPENDIX F

PHENOTYPIC AND GENOTYPIC CORRELATION COEFFICIENTS

Table F1. Phenotypic correlation coefficients among 12 traits evaluated on 188 F_2 plants of the SE-40×LE-37 maize population grown near Ames, IA in 2000.

Trait †		ED	CD	KD	KRN	K/5CM	KWT	GY	PLTHT	TB	Pgdd	Sgdd
		cm	cm	cm	no.	no.	g	g plant^{-1}	cm	no.	gdd	gdd
EL	cm	−0.05	0.08	−0.18*	−0.25**	−0.26**	0.30**	0.63**	0.39**	−0.22**	−0.16*	−0.23**
ED	cm		0.73**	0.59**	0.58**	−0.20**	0.40**	0.45**	0.08	0.12	−0.41**	−0.39**
CD	cm			−0.11	0.40**	−0.32**	0.29**	0.33**	0.13	−0.02	−0.39**	−0.35**
KD	cm				0.37**	0.08	0.24**	0.26**	−0.03	0.20**	−0.14	−0.18*
KRN	no.					−0.14*	−0.19*	0.07	−0.08	0.36**	−0.20**	−0.12
K/5CM	no.						−0.39**	−0.17*	−0.18*	0.04	0.09	0.10
KWT	g							0.61**	0.20**	−0.17*	−0.33**	−0.40**
GY	g plant^{-1}								0.40**	−0.18*	−0.46**	−0.48**
PLTHT	cm									−0.34**	−0.08	−0.08
TB	no.										−0.04	−0.08
Pgdd	gdd											0.90**

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

† EL = ear length, ED = ear diameter, CD = cob diameter, KD = kernel depth, KRN = kernel-row number, K/5CM = kernels per 5 cm of EL, KWT = weight of 300 kernels, GY = grain yield, PLTHT = plant height, TB = number of secondary tassel branches, and Pgdd and Sgdd = growing degree days (°C) when each plant showed male or female anthesis, respectively.

Table F2. Phenotypic correlation coefficients among 12 traits evaluated on 188 $F_{2:3}$ progeny of the SE-40×LE-37 maize population grown near Ames, IA in 2001.

Trait †		ED	CD	KD	KRN	K/5CM	KWT	GY	PLTHT	TB	Pgdd	Sgdd
		cm	cm	cm	no.	no.	g	g plant^{-1}	cm	no.	gdd	gdd
EL	cm	–0.19**	0.00	–0.24**	–0.17*	–0.17*	–0.04	0.30**	0.27**	0.08	–0.01	0.01
ED	cm		0.61**	0.65**	0.74**	0.10	0.25**	0.42**	0.00	0.13	–0.28**	–0.16*
CD	cm			–0.20**	0.45**	–0.29**	0.20**	–0.07	0.05	0.16*	0.09	0.27**
KD	cm				0.48**	0.40**	0.12	0.58**	–0.06	0.01	–0.42**	–0.45**
KRN	no.					0.23**	–0.19**	0.35**	–0.02	0.11	–0.27**	–0.16*
K/5CM	no.						–0.56**	0.25**	–0.19**	–0.03	–0.43**	–0.37**
KWT	g							0.10	0.23**	–0.09	0.19**	0.10
GY	g plant^{-1}								0.16*	–0.12	–0.50**	–0.65**
PLTHT	cm									0.16*	0.12	0.12
TB	no.										0.18**	0.31**
Pgdd	gdd											0.82**

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

† EL = ear length, ED = ear diameter, CD = cob diameter, KD = kernel depth, KRN = kernel-row number, K/5CM = kernels per 5 cm of EL, KWT = weight of 300 kernels, GY = grain yield, PLTHT = plant height, TB = number of secondary tassel branches, and Pgdd and Sgdd = growing degree days (°C) when 50% of the plants showed male or female anthesis, respectively.

Table F3. Phenotypic correlation coefficients among 10 traits evaluated on 188 $F_{2:3}$ progeny of the SE-40×LE-37 maize population grown near Ankeny, IA in 2001.

Trait †		ED	CD	KD	KRN	K/5CM	KWT	GY	PLTHT	TB
		cm	cm	cm	no.	no.	g	g plant^{-1}	cm	no.
EL	cm	–0.14	–0.10	–0.07	–0.11	–0.09	0.02	0.37**	0.23**	0.01
ED	cm		0.59**	0.64**	0.74**	0.19**	0.14*	0.48**	–0.02	0.05
CD	cm			–0.24**	0.37**	–0.30**	0.15*	–0.13	0.06	0.19*
KD	cm				0.53**	0.52**	0.03	0.70**	–0.08	–0.12
KRN	no.					0.38**	–0.27**	0.48**	–0.02	0.05
K/5CM	no.						–0.58**	0.48**	–0.24**	–0.16*
KWT	g							–0.02	0.18**	–0.04
GY	g plant^{-1}								0.14	–0.19**
PLTHT	cm									–0.02

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

† EL = ear length, ED = ear diameter, CD = cob diameter, KD = kernel depth, KRN = kernel-row number, K/5CM = kernels per 5 cm of EL, KWT = weight of 300 kernels, GY = grain yield, PLTHT = plant height, and TB = number of secondary tassel branches.

Table F4. Phenotypic correlation coefficients among 10 traits evaluated on 188 $F_{2:3}$ progeny of SE-40×LE-37 grown near Crawfordsville, IA in 2001.

Trait †		ED	CD	KD	KRN	K/5CM	KWT	GY	PLTHT	TB
		cm	cm	cm	no.	no.	g	g plant^{-1}	cm	no.
EL	cm	−0.25**	−0.09	−0.26**	−0.20**	−0.17*	−0.01	0.22**	0.33**	0.05
ED	cm		0.71**	0.62**	0.72**	0.00	0.23**	0.41**	−0.03	0.17*
CD	cm			−0.11	0.49**	−0.26**	0.20**	0.01	0.05	0.15*
KD	cm				0.47**	0.30**	0.10	0.58**	−0.10	0.08
KRN	no.					0.21**	−0.25**	0.40**	−0.12	0.16*
K/5CM	no.						−0.54**	0.17*	−0.27**	0.05
KWT	g							0.17*	0.30**	−0.13
GY	g plant^{-1}								0.13	−0.08
PLTHT	cm									0.08

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

† EL = ear length, ED = ear diameter, CD = cob diameter, KD = kernel depth, KRN = kernel-row number, K/5CM = kernels per 5 cm of EL, KWT = weight of 300 kernels, GY = grain yield, PLTHT = plant height, and TB = number of secondary tassel branches.

Table F5. Phenotypic correlation coefficients among 10 traits evaluated on 188 $F_{2:3}$ progeny of the SE-40×LE-37 maize population grown near Lewis, IA in 2001.

Trait †		ED	CD	KD	KRN	K/5CM	KWT	GY	PLTHT	TB
		cm	cm	cm	no.	no.	g	g plant^{-1}	cm	no.
EL	cm	–0.02	–0.03	–0.01	–0.19*	–0.10	0.10	0.36**	0.28**	–0.04
ED	cm		0.85**	0.73**	0.48**	0.45**	0.33**	0.57**	0.00	–0.04
CD	cm			0.25**	0.27**	0.30**	0.35**	0.25**	0.03	–0.01
KD	cm				0.53**	0.44**	0.15*	0.71**	–0.04	–0.06
KRN	no.					0.23**	–0.24**	0.44**	–0.13	–0.04
K/5CM	no.						0.07	0.39**	–0.11	–0.12
KWT	g							0.14	0.12	–0.08
GY	g plant^{-1}								0.12	–0.28**
PLTHT	cm									0.18*

*, ** Significant at the 0.05 and 0.01 probability levels, respectively

† EL = ear length, ED = ear diameter, CD = cob diameter, KD = kernel depth, KRN = kernel-row number, K/5CM = kernels per 5 cm of EL, KWT = weight of 300 kernels, GY = grain yield, PLTHT = plant height, and TB = number of secondary tassel branches.

Table F6. Phenotypic correlation coefficients among 10 traits evaluated on 188 $F_{2:3}$ progeny of the SE-40×LE-37 maize population grown near Ames, Ankeny, Crawfordsville, and Lewis, IA in 2001.

Trait †		ED	CD	KD	KRN	K/5CM	KWT	GY	PLTHT	TB
		cm	cm	cm	no.	no.	g	g plant^{-1}	cm	no.
EL	cm	–0.23**	–0.08	–0.24**	–0.25**	–0.22**	0.02	0.25**	0.27**	0.03
ED	cm		0.72**	0.69**	0.75**	0.24**	0.16*	0.48**	–0.09	0.07
CD	cm			–0.01	0.48**	–0.17*	0.18*	–0.01	0.01	0.13
KD	cm				0.57**	0.53**	0.05	0.70**	–0.14	–0.04
KRN	no.					0.31**	–0.28**	0.43**	–0.09	0.09
K/5CM	no.						–0.46**	0.42**	–0.29**	–0.10
KWT	g							0.03	0.23**	–0.13
GY	g plant^{-1}								0.10	–0.21**
PLTHT	cm									0.10

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

† EL = ear length, ED = ear diameter, CD = cob diameter, KD = kernel depth, KRN = kernel-row number, K/5CM = kernels per 5 cm of EL, KWT = weight of 300 kernels, GY = grain yield, PLTHT = plant height, and TB = number of secondary tassel branches.

Table F7. Genotypic correlation coefficients (± approximate standard error) among 10 traits evaluated on 188 $F_{2:3}$ lines of the SE-40×LE-37 maize population grown near Ames, Ankeny, Crawfordsville, and Lewis, IA in 2001.

Trait †		ED	CD	KD	KRN	K/5CM	KWT	GY	PLTHT	TB
		cm	cm	cm	no.	no.	g	g plant^{-1}	cm	no.
EL	cm	–0.28 ± 0.11	–0.10 ± 0.08	–0.29 ± 0.11	–0.28 ± 0.11	–0.27 ± 0.11	0.02 ± 0.07	0.22 ± 0.10	0.27 ± 0.11	0.03 ± 0.07
ED	cm		0.70 ± 0.25	0.71 ± 0.24	0.82 ± 0.27	0.23 ± 0.11	0.09 ± 0.08	0.49 ± 0.17	–0.13 ± 0.08	0.07 ± 0.08
CD	cm			0.00 ± 0.07	0.55 ± 0.19	–0.27 ± 0.12	0.12 ± 0.08	–0.04 ± 0.07	0.00 ± 0.07	0.14 ± 0.08
KD	cm				0.61 ± 0.19	0.60 ± 0.20	0.02 ± 0.07	0.73 ± 0.24	–0.18 ± 0.09	–0.04 ± 0.07
KRN	no.					0.35 ± 0.13	–0.32 ± 0.13	0.44 ± 0.15	–0.10 ± 0.07	0.10 ± 0.08
K/5CM	no.						–0.58 ± 0.21	0.47 ± 0.17	–0.35 ± 0.13	–0.11 ± 0.08
KWT	g							–0.01 ± 0.07	0.25 ± 0.11	–0.16 ± 0.09
GY	g plant^{-1}								0.08 ± 0.08	–0.23 ± 0.10
PLTHT	cm									0.11 ± 0.08

† EL = ear length, ED = ear diameter, CD = cob diameter, KD = kernel depth, KRN = kernel-row number, K/5CM = kernels per 5 cm of EL, KWT = weight of 300 kernels, GY = grain yield, PLTHT = plant height, and TB = number of secondary tassel branches.

APPENDIX G

HERITABILITIES ESTIMATED BY F_2–$F_{2:3}$ REGRESSION

Table G1. Heritabilities (h^2) (†) and 95%-confidence interval (CI) for 12 traits estimated by regressing the $F_{2:3}$–progeny means from four Iowa environments in 2001 and the mean environment onto the F_2–plant values obtained from the SE-40×LE-37 maize population grown near Ames, IA in 2000.

Environment (Env.)	EL‡		ED		CD		KD		KRN		K/5CM	
	h^2	CI	h^2	CI	h^2	CI	h^2	CI	h^2	CI	h^2	CI
Ames	0.37	0.29–0.44	0.44	0.36–0.51	0.36	0.28–0.44	0.31	0.20–0.42	0.38	0.32–0.45	0.26	0.16–0.36
Ankeny	0.37	0.29–0.44	0.39	0.30–0.47	0.38	0.30–0.46	0.27	0.16–0.39	0.26	0.19–0.33	0.27	0.16–0.38
Crawfordsville	0.36	0.28–0.43	0.42	0.34–0.50	0.40	0.32–0.48	0.30	0.21–0.40	0.37	0.31–0.43	0.28	0.17–0.39
Lewis	0.38	0.31–0.45	0.46	0.28–0.63	0.32	0.17–0.48	0.35	0.21–0.49	0.31	0.25–0.37	0.16	-0.01–0.32
Mean	0.37	0.30–0.44	0.42	0.34–0.51	0.37	0.29–0.44	0.31	0.21–0.41	0.33	0.28–0.39	0.24	0.14–0.34

Table G1. (cont.)

Environment (Env.)	KWT		GY		PLTHT		TB		Pgdd		Sgdd	
	h^2	CI	h^2	CI	h^2	CI	h^2	CI	h^2	CI	h^2	CI
Ames	0.25	0.13–0.37	0.43	0.33–0.54	0.46	0.37–0.55	0.43	0.36–0.51	0.81	0.70–0.92	0.96	0.83–1.09
Ankeny	0.29	0.18–0.39	0.46	0.33–0.57	0.54	0.47–0.62	0.35	0.27–0.42				
Crawfordsville	0.17	0.06–0.28	0.33	0.25–0.41	0.52	0.42–0.62	0.38	0.31–0.45				
Lewis	0.18	0.00–0.37	0.37	0.26–0.47	0.48	0.39–0.57	0.30	0.23–0.38				
Mean	0.22	0.12–0.32	0.39	0.31–0.48	0.50	0.43–0.57	0.37	0.30–0.43				

† h^2 = linear regression coefficient (b) when $F_{2:3}$ progeny are regressed onto F_2 (parent) values (Fernandez and Miller, 1985).

‡ EL = ear length, ED = ear diameter, CD = cob diameter, KD = kernel depth, KRN = kernel-row number, K/5CM = kernels per 5 cm of EL, KWT = weight of 300 kernels, GY = grain yield, PLTHT = plant height, TB = number of secondary tassel branches, and Pgdd and Sgdd = growing degree days (°C) when each plant showed male or female anthesis, respectively.

APPENDIX H

QTL DETECTED IN THE $F_{2:3}$ MEAN AND INDIVIDUAL ENVIRONMENTS

Table H1. Summary of QTL positions (†) and genetic effects, identified among 188 $F_{2:3}$ progeny from the SE-40×LE-37 maize population, for six traits evaluated at four Iowa environments in 2001 and the mean environment analysis.

	Mean			Ames			Ankeny			Crawfordsville			Lewis		
Chrom.	Pos. ‡	*a* §	*d* ¶	Pos.	*a*	*d*	Pos.	*a*	*d*	Pos.	*a*	*d*	Pos.	*a*	*d*
	Ear length (EL, cm)														
1	4–24	0.3**	0.1	10–30	0.6**	0.0							24–44	0.6**	0.2
1	54–74	0.5**	0.2				48–68	0.7**	0.0	52–72	0.6**	–0.1			
1							122–142	–0.1	0.5**						
1	150–170	–0.4**	0.3*				158–178	–0.5**	–0.1	152–172	–0.3**	0.7**	154–174	–0.4**	0.2
2	20–40	0.2	0.4**												
2							50–70	0.4**	0.1						
2													74–94	0.5**	0.0
3	12–32	–0.3**	–0.1												
3	92–112	0.7**	0.0				108–128	0.6**	0.2	78–98	0.4**	0.0	104–124	0.6**	–0.1
3				150–170	0.2	0.4*									
4	62–82	–0.4**	0.2				58–78	–0.6**	0.0						
5	66–86	0.6**	0.3	78–98	0.7**	0.6**	72–92	0.4**	0.1	76–96	0.6**	0.3	58–78	0.5**	0.4*
5	118–138	0.3**	0.3*				126–146	0.2	0.4*	120–140	0.4**	0.3			

† QTL identified in different environments that share a row are considered the same based on overlapping positions (Pos.)

‡ Position in centimorgans (cM) from the distal end of the short chromosome arm. A QTL position is a 20-cM interval symmetrically placed over the highest LOD value.

§ *a* = additive effect of QTL. Positive and negative (–) values indicated an allele from LE-37 or SE-40, respectively, increased the trait's phenotype.

¶ *d* = dominance deviation of QTL. Positive and negative (–) values indicated over-dominance and under-dominance, respectively.

Phenotypic variation explained by the multiple-QTL model adjusted for degrees of freedom.

Table III. (cont.)

	Mean			Ames			Ankeny			Crawfordsville			Lewis		
Chrom.	Pos.	*a*	*d*	Pos.	*a*	*d*	Pos.	*a*	*d*	Pos.	*a*	*d*	Pos.	*a*	*d*
6	0–10	0.5**	0.0	0–10	0.6**	0.0	0–10	0.5**	0.1	0–10	0.7**	0.1	0–10	0.6**	0.2
6	90–110	0.7**	0.2	90–110	0.7**	0.2	90–110	0.5**	0.3	90–110	0.7**	0.0	92–112	0.7**	0.0
6	136–156	0.6**	0.2	138–158	0.6**	–0.1	134–154	0.7**	0.2	136–156	0.6**	0.1	132–152	0.5**	0.0
7				0–10	0.5**	–0.3				0–12	0.3*	–0.4*			
7	10–30	0.3**	0.2				20–40	0.4**	0.1						
7	56–76	0.4**	–0.2	48–68	0.6**	0.0				44–64	0.4**	–0.1	54–74	0.5**	–0.3*
7							82–102	0.7**	0.0						
7							104–124	–0.7**	0.0						
9				10–30	0.6**	0.4**									
9	38–58	–0.3	0.6**												
9	50–70	0.7**	–0.3							50–70	0.7**	0.2	52–72	0.5**	0.3
9				76–96	0.4**	0.3									
10				38–58	0.0	0.6**				38–58	–0.3*	0.6**			
σ_p^2 #	70%			62%			60%			58%			54%		
	Kernels per 5 cm of EL (K/5CM, no.)														
1							98–118	0.3**	0.1	94–114	0.3**	–0.1			
1	118–138	0.2**	–0.2**												
1	204–224	–0.3**	0.2*	206–226	–0.4**	0.2	206–226	–0.3**	0.2	198–218	–0.3**	0.4**			
2	48–68	–0.4**	0.1	48–68	–0.4**	0.1	50–70	–0.3**	0.2	52–72	–0.4**	0.0			
2	142–162	–0.2**	0.2*	130–150	–0.4**	0.1	126–146	0.3**	0.2	122–142	–0.3**	0.1			

Table III. (cont.)

	Mean			Ames			Ankeny			Crawfordsville			Lewis		
Chrom.	Pos.	*a*	*d*	Pos.	*a*	*d*	Pos.	*a*	*d*	Pos.	*a*	*d*	Pos.	*a*	*d*
3	36–56	0.2**	0.2	38–58	0.2*	0.4**				26–46	0.1	0.4**			
3							160–180	0.1	0.3*						
4				62–82	–0.3**	0.1				66–86	–0.6**	0.2			
4				88–108	0.4**	0.0				84–104	0.5**	–0.1			
5	90–110	–0.2**	0.0				88–108	–0.4**	0.2				90–110	–0.3**	–0.2
6	18–38	–0.2**	0.0	22–42	–0.3**	0.0	14–34	–0.4**	–0.1	28–48	–0.2**	–0.1			
7	84–104	–0.1	0.3**	86–106	–0.2**	0.3*				88–108	–0.1	0.5**	68–88	–0.3**	0.4**
8	0–12	0.2**	0.0										0–10	0.3**	–0.4**
8	34–54	–0.3**	0.1				32–52	–0.4**	0.1	32–52	–0.3**	0.0			
9	40–60	–0.3**	0.2*	44–64	–0.3**	0.0	46–66	–0.4**	0.1	54–74	–0.3**	–0.2			
10	14–34	0.2**	0.2*										06–26	–0.1	0.5**
10													48–68	0.3**	0.2
10							72–92	0.4**	–0.1						
σ_p^2	62%			52%			48%			48%			27%		
	Grain yield (GY, g plant $^{-1}$)														
1				210–230	–3	8**									
3				152–172	–3	7**									
5	90–110	–12**	8**	90–110	–11**	8**	92–112	–18**	5	90–110	–8**	5**	90–110	–11**	9**
5							106–126	4	11*						

Table III. (cont.)

	Mean			Ames			Ankeny			Crawfordsville			Lewis		
Chrom.	Pos.	*a*	*d*	Pos.	*a*	*d*	Pos.	*a*	*d*	Pos.	*a*	*d*	Pos.	*a*	*d*
6	112–132	4**	3	106–126	7**	1									
10	10–30	2	7**							12–32	0	8**	10–30	2	8**
σ_p^2	36%			29%			26%			22%			28%		
	Kernel weight (KWT, g $300k^{-1}$)														
1													88–108	–2**	–1
1													168–188	2**	1
1	204–224	3**	0	210–230	5**	0	206–226	4**	0	204–224	4**	–1			
2							10–30	2**	3**						
3													42–62	–3**	–1
3	68–88	–2**	0				78–98	–2**	0						
3	130–150	–3**	2	124–144	–4**	1	130–150	–3**	3**	124–144	–3**	1			
4	88–108	–3**	0				84–104	–4**	1				102–122	–3**	–2
5	74–94	–2**	0	70–90	–3**	1									
5	166–186	–2**	0												
6	26–46	2**	1							18–38	2**	0	14–34	2*	–3**
6				54–74	2**	–3*									
7				74–94	–3**	–2				70–90	–3**	–1			
7	126–146	1**	2**				128–148	2**	2*				126–146	2**	1
8				24–44	2**	1				30–50	2**	1	40–60	2**	0
9	50–70	3**	0	46–66	3**	0	50–70	3**	–1	50–70	3**	1	50–70	4**	0

Table III. (cont.)

	Mean			Ames			Ankeny			Crawfordsville			Lewis		
Chrom.	Pos.	*a*	*d*	Pos.	*a*	*d*	Pos.	*a*	*d*	Pos.	*a*	*d*	Pos.	*a*	*d*
10										18–38	–3**	1			
σ_p^2	43%			41%			46%			30%			36%		
	Kernel-row number (KRN, no.)														
1							0–12	–0.3**	0.3*	0–16	–0.4**	0.2			
1	52–72	–0.7**	0.1				66–86	–0.4**	0.1	58–78	–0.5**	0.1	66–86	–0.6**	0.1
1										108–128	–0.4**	0.1			
1										150–170	0.2*	0.4**			
1	202–222	–0.4**	0.2	210–230	–0.5**	0.2				202–222	–0.6**	0.2			
1	236–256	–0.3**	0.0				232–252	–0.7**	0.0				224–244	–0.6**	0.2
2	0–14	–0.3**	0.3*	0–12	–0.5**	0.2	0–16	–0.3**	0.4*						
2													20–40	–0.4**	0.1
2							124–144	–0.1	0.5**						
3	148–168	–0.3**	0.1	154–174	–0.3**	0.2				136–156	–0.3**	0.1	154–174	–0.4**	0.0
4	84–104	0.4**	–0.1	82–102	0.5**	–0.1							84–104	0.5**	–0.1
4										106–126	0.5**	0.1			
5										58–78	–0.3**	0.1			
5	84–104	–0.5**	0.2	90–110	0.4**	0.3*	86–106	0.5**	0.1	92–112	–0.2*	0.2	90–110	–0.4**	0.2
6										32–52	–0.4**	0.0	16–36	–0.3**	0.1
7	90–110	–0.2**	0.3**												
7				124–144	–0.3**	0.1							128–148	–0.3**	0.0

Table III. (cont.)

	Mean			Ames			Ankeny			Crawfordsville			Lewis		
Chrom.	Pos.	*a*	*d*	Pos.	*a*	*d*	Pos.	*a*	*d*	Pos.	*a*	*d*	Pos.	*a*	*d*
8	6–26	0.2*	0.0							0–18	0.5**	0.0	6–26	0.3**	0.0
8				36–56	0.3**	-0.1									
9										0–10	0.3**	0.0			
9	38–58	-0.4**	-0.1	40–60	-0.5**	-0.1	46–66	-0.7**	0.0	40–60	-0.4**	-0.2	40–60	-0.5**	0.1
9	88–108	-0.2**	0.1												
10	78–98	-0.3**	0.1	72–92	-0.5**	0.1				82–102	-0.6**	0.2			
σ_p^2	63%			53%			48%			61%			53%		
	Kernel depth (KD, cm)														
1							0–12	-0.02**	0.01						
1				44–64	-0.02**	0.01									
1										146–166	0.02*	0.02*			
1	210–230	-0.01*	0.03**	210–230	-0.02**	0.02							206–226	-0.03**	0.02
2	36–56	-0.03**	0.02*	40–60	-0.04**	0.02	28–48	-0.03**	0.03*	34–54	-0.02*	0.03**			
2										132–152	-0.03**	0.01			
3	64–84	-0.01	0.03**	66–86	-0.02**	0.02									
3	132–152	-0.03**	-0.01							126–146	-0.03**	-0.02			
3				154–174	-0.03**	0.02							154–174	-0.03**	0.02
4							30–50	0.03**	0.00				24–44	0.03**	-0.01
4							72–92	-0.03**	-0.01						
5										62–82	-0.05**	0.00			

Table III. (cont.)

	Mean			Ames			Ankeny			Crawfordsville			Lewis		
Chrom.	Pos.	*a*	*d*	Pos.	*a*	*d*	Pos.	*a*	*d*	Pos.	*a*	*d*	Pos.	*a*	*d*
5	82–102	–0.06**	0.02*	78–98	–0.05**	0.02*	90–110	–0.05**	0.01				94–114	–0.05**	0.04**
5	170–190	–0.02**	0.00	160–180	–0.04**	0.00				168–188	–0.03**	0.00			
6										14–34	–0.03**	0.01			
7				84–104	–0.01*	0.01							84–104	–0.02**	0.04**
8										84–104	–0.03**	0.02*			
9				70–90	–0.02**	0.00									
10				10–30	0.01	0.02*	16–36	0.02**	0.01						
σ_p^2	46%			46%			35%			38%			31%		

APPENDIX I

PEDIGREE TREE OF THE IOWA LONG-EAR SYNTHETIC PROGENITORS

Appendix 11. Pedigree of each progenitor of the Iowa Long-Ear Synthetic (BSLE).

BSLE Parent	Parent Pedigree	Grand Parent	Grand Parent Pedigree	Great-Grand Parent	Great-Grand Parent Pedigree	Great-Great-Grand Parent	Great-Great-Grand Parent Pedigree
B50	(M14/A206)/Oh04C	M14	BR10/R8	BR10	**Funk Yellow Dent** †		
				R8	**Texas Sure Cropper**		
		A206	(C11/C23)/C11[2]	C11	**Minnesota No.13**		
				C23	**Reid Yellow Dent**		
		Oh04c	C.I.14/Oh04	C.I.14	?		
				Oh04	?		
B55	Oh45/W92	Oh45	Oh40B/W8	Oh40B	**Lancaster Sure Crop**		
				W8	M13/111.A48	M13	**Minnesota No.13**
						111.A48	?
		W92	*Pioneer 322*	N/A	**Reid Yellow Dent**		
				N/A	**Reid Yellow Dent**		
				N/A	**Illinois Two Ear**		
				N/A	**Illinois Low Ear**		
B56	Alph/38-11		**Alph Landrace**				
		38-11	176A (Outcross)		**Funk Yellow Dent**		
B217*wx*	(H.O./B10)/B10)-1-1-2-1		**High Oil**				
		B10	SSS507-193-4-1-1		**Iowa Stiff Stalk Syn.**		
C103	**Lancaster Sure Crop**						
N22A	**Krug Yellow Dent**						

† Pedigrees in bold text are populations or synthetics, and represent the end of pedigree branch.

Appendix II. (cont.)

BSLE Parent	Parent Pedigree	Grand Parent	Grand Parent Pedigree	Great-Grand Parent	Great-Grand Parent Pedigree	Great-Great-Grand Parent	Great-Great-Grand Parent Pedigree
N25	**Reid Yellow Dent**						
Oh29	Oh28/Ia.159L1	Oh28	(C112-1/Oh920)/(111.A/111.B)	C112-1	**Leaming ?**		
				Oh920	?		
				111.A	?		
				111.B	?		
		Ia.159L1	Iodent		**Reid Yellow Dent**		
W-17R-B	same as OS420	OS420	**Osterland Yellow Dent**				
Lancaster-34	**Lancaster Sure Crop**						
(B15/B18)-16		B15	(Wf9/D17)-561	Wf9	**Reid Yellow Dent**		
				D17	?		
		B18	M4-345		**Midland Yellow Dent**		
(L317/C.I.187-2)-1-1-9		L317	**Lancaster Sure Crop**				
		C.I.187-2	**Krug Yellow Dent**				

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